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# POPULATION STATUS AND PATTERNS OF DISTRIBUTION AND PRODUCTIVITY OF KITTIWAKES ON ST. GEORGE ISLAND, ALASKA.

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

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DOCTOR OF PHILOSOPHY

By

Stewart Dean Kildaw, B.S., M.Sc.

Fairbanks, Alaska

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POPULATION STATUS AND PATTERNS OF DISTRIBUTION AND PRODUCTIVITY OF KITTIWAKES ON ST. GEORGE ISLAND, ALASKA

By

Stewart Dean Kildaw

RECOMMENDED:

Advisory Committee Chair

Department Head, Biology and Wildlife

APPROVED:

Dean, College of Science, Engineering and Mathematics

Dean of the Graduate School

Date

## ABSTRACT

I studied populations, distributions, and reproductive performance of red-legged and black-legged kittiwakes on St. George Island in the summers of 1993 - 1995, where populations of both species have experienced generally poor reproductive performance and population declines of ca. 40% over the past 20 years. In 1995, I conducted a whole-island census of kittiwakes on St. George Island and found estimated breeding populations of 193,930 red-legged kittiwakes (81% of their global population), and 62,568 black-legged kittiwakes. In addition, I analyzed census trends on 51 land-based census plots on St. George Island and found that numbers of both species have stabilized in recent years.

I experimentally evaluated the hypothesis that nesting red-legged kittiwakes on St. George Island are competitively displaced by larger-bodied black-legged kittiwakes to narrower rock ledges and higher elevations. I determined nest-site preferences of both species by attaching narrow and wide artificial nesting ledges within high- and low-elevation areas of St. George Island and found no evidence of competitive displacement: red-legged kittiwakes preferred narrow ledges, black-legged kittiwakes preferred wide ledges, and both species preferred ledges in areas where conspecifics nested at high density.

Multiple regression analyses suggested that kittiwakes breed earlier and more successfully in summers preceded by cold winters and that inter-annual variability in kittiwake breeding success was unrelated to weather conditions during the breeding season itself. These results suggest that winter weather has indirect effects on breeding kittiwakes by influencing prey abundance several months later. Furthermore, strong winds impaired growth rates of kittiwake chicks in exposed nest sites and the growth of black-legged kittiwake chicks relative to red-legged kittiwake chicks.

I identified two prominent patterns of within-colony spatial variability in kittiwake productivity and suggest that patchy "bird quality" or localized "information

neighborhoods" may be responsible because traditional explanations do not apply. The "information neighborhood" is a new hypothesis which proposes that individuals are influenced by the breeding status of neighbors because their status represents an additional source of information about current breeding conditions that can be used to better tailor parental investment.

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## GENERAL INTRODUCTION

Kittiwakes are small, cliff nesting gulls that are apex consumers in marine ecosystems. Red-legged and black-legged kittiwakes are ecologically similar species that share several traits: they avoid terrestrial predators by building nests on small rock projections on vertical cliff faces (Cullen 1957); they are members of a guild of surface-feeding seabirds, capturing prey (small fish and large zooplankton) within the uppermost 1 m of the water column; they are long-lived, exhibit a low annual reproductive output, and exhibit high levels of both mate and nest-site fidelity (Byrd and Williams 1993, Baird 1994).

In contrast, these two species differ in several biologically significant ways. Red-legged kittiwakes are smaller-bodied than black-legged kittiwakes and have proportionately smaller bills and larger eyes (Byrd and Williams 1993). Compared to black-legged kittiwakes, red-legged kittiwakes breed on narrower rock ledges and build nests that are smaller in diameter and composed of a thicker base of adhesive mud (Squibb and Hunt 1983). Clutch size differs between species: red-legged kittiwakes rarely lay more than one egg whereas black-legged kittiwakes typically lay two and occasionally three eggs (Byrd and Williams 1993). The diet of the two species also differs markedly. Red-legged kittiwakes feed primarily on energy-rich myctophid fishes (Byrd and Williams 1993, Lance 1996) which they encounter at night at the surface layer of deep oceanic waters, while black-legged kittiwakes have a more generalized diet and forage on prey species within comparatively shallow continental shelf waters. Lastly, the distributions of the two species differ markedly. Whereas black-legged kittiwakes are abundant and widely distributed throughout the north temperate latitudes (Baird 1994), red-legged kittiwakes are endemic to the Bering Sea and breed at only four known locations (Byrd et al. 1997). Furthermore, more than 80% of world's breeding population of red-legged kittiwakes is localized on St. George Island (the southern-most of the Pribilof Islands) in the south-eastern Bering Sea (Byrd et al 1997), where they are

concentrated within the highest-elevation coastal cliffs on the island (Hickey and Craighead 1977).

In general, the productivity of kittiwakes in North Pacific has been lower and more variable than that of black-legged kittiwakes in the North Atlantic. In particular, populations of both species on St. George Island experienced generally poor productivity during the 1980's and population declines of 40% between the 1976 and the mid-late 1980's and. Other apex consumers in the Bering Sea have also experienced dramatic population reductions over the past two decades (Merrick et al. 1987, York and Kosloff 1987, Pitcher 1990), suggesting that ecosystem-wide changes may have contributed to declines in kittiwake populations on St. George Island. The red-legged kittiwake is currently considered a "species of concern" because its breeding distribution is restricted and because of the questionable status of its population on St. George Island. Investigations described within this thesis were conducted to further our understanding of the population status and patterns of distribution and productivity of kittiwakes breeding on St. George Island.

Our present understanding of the importance of St. George Island to the global breeding population of red-legged kittiwakes is based on an imprecise whole-island census conducted in 1976 (Hickey and Craighead 1977). In Chapter 1, I present the results of a whole-island census of kittiwakes on St. George Island in 1995, and critically evaluate trends in kittiwake numbers on land-based count plots between 1976 and 1995.

The nesting distribution of the two kittiwake species on St. George Island differs in two key ways. Red-legged kittiwakes are concentrated within high elevation areas and nest on narrower rock ledges than do black-legged kittiwakes (Hickey and Craighead 1977, Squibb and Hunt 1983). In Chapter 2, I determine whether the distribution of red-legged kittiwakes on St. George Island is shaped by competitive displacement by larger-bodied black-legged kittiwakes.

The remaining two chapters address factors that influence breeding success of

kittiwakes on St. George Island. Although variable productivity of kittiwakes is usually attributed to fluctuations in prey abundance, weather may have direct and indirect effects on prey abundance and kittiwake foraging efficiency in a number of ways. In Chapter 3, I evaluate the contribution of weather to inter-annual variability in kittiwake productivity and the effects of strong winds on growth rates of kittiwake chicks.

In addition to inter-annual variability in productivity, kittiwakes exhibit marked with-colony variability in productivity on St. George Island. In Chapter 4, I describe spatial patterns of within-colony productivity and evaluate several hypotheses which potentially explain them.

# A CENSUS OF KITTIWAKES ON ST. GEORGE ISLAND, ALASKA, IN 1995[1]


## SUMMARY

In late July 1995, I conducted a whole-island census of kittiwakes on St. George Island, Alaska, by photographing cliffs around the entire perimeter of the island and later counting birds directly from photographic negatives using a dissecting microscope. Raw counts from 825 cliff-photographs were adjusted by observability and mis-classification correction factors for kittiwakes and were partitioned into Red-legged Kittiwake and Black-legged Kittiwake fractions using the relative abundance of the two species determined from 426 land-based plots. Whole-island totals were 156,902 ± 27,956 (95% CI) Red-legged Kittiwakes and 45,972 ± 10,860 (95% CI) Black-legged Kittiwakes. These totals are minimum estimates of the colony attendance of kittiwakes on St. George Island because observability correction factors likely underestimate the number of misclassified kittiwakes on the highest elevation photographs and because some cliff area could not be photographed from the water. I transformed my census total for red-legged Kittiwakes on St. George Island to a breeding population estimate (96,965 nests = 193,930 individuals) and estimated that Red-legged Kittiwakes on St. George Island comprise 81% of a global breeding population of 239,060 Red-legged Kittiwakes. A census of kittiwakes on 51 "common" land-based plots on St. George Island in 1995 produced population totals of 2480 Red-legged Kittiwakes and 694 Black-legged Kittiwakes. Counts in 1995 were 70% and 77% of counts in 1976 for Red-legged and Black-legged Kittiwakes, respectively. After a period of marked decline between 1976 and the late-1980's, land-based counts of both species on St. George Island have stabilized in recent years.


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[1] Prepared for publication in *Bird Conservation International* as: Kildaw S. D. A census of kittiwakes on St. George Island, Alaska, in 1995.

# INTRODUCTION

St. George Island, Alaska, is the breeding site of one of the largest aggregations of cliff-nesting seabirds in the North Pacific. In 1976, Hickey and Craighead (1977) conducted counts of cliff-nesting seabirds on St. George Island and reported a total of 2.1 million birds, including an estimated 222,700 Red-legged Kittiwakes (*Rissa brevirostris*) and 71,500 Black-legged Kittiwakes *(R. tridactyla)*. Although such "attendance" counts represent an unknown and varying proportion of the total population of kittiwakes that are associated breeding colonies, they are an easily-obtained index of population size that is less sensitive to inter-annual variability in reproductive performance than are other potential indices of kittiwake populations (e.g. counts of nests, Hatch and Hatch 1988).

Over the past 20 years, population trends of both species of kittiwakes on St. George Island have been monitored on land-based census plots that were established in 1976 by Hickey and Craighead (1977). By the mid-late 1980's, numbers of both species had declined to roughly 60% of their levels in 1976 (Dragoo and Sundseth 1993). In contrast, counts of Red-legged Kittiwakes more than doubled between the mid-1970's and the late-1980's on Buldir Island, and more than tripled between the mid-1970's and the early-1990's at Bogoslof Island. (Byrd et al. 1997).

Unlike the Black-legged Kittiwake, which has a circumpolar breeding distribution and a global population that numbers in the millions, the Red-legged Kittiwake is endemic to the Bering Sea. Approximately 80% of the global population of Red-legged Kittiwakes breeds on St. George Island, one of only 4 known breeding locations for this species (Byrd et al. 1997). Because Red-legged Kittiwakes on St. George Island experienced population declines and generally poor reproductive success during the 1980's (Dragoo and Sundseth 1993), the U. S. Fish and Wildlife Service considers the Red-legged Kittiwake a "species of concern", a potential precursor to "threatened" or "endangered" classification under the Endangered Species Act.

An updated whole-island census of Red-legged Kittiwakes is needed because our present understanding of the importance of St. George Island to the global Red-legged

Kittiwake population is dependent on a crude, whole-island estimate that is 20 years old (Hickey and Craighead 1977). The purpose of this study was three-fold: a) to conduct a whole-island census of kittiwakes on St George Island, b) to census kittiwakes on land-based plots, and c) to evaluate population trends of kittiwakes over the past 20 years on St. George Island.

## METHODS

### *Study Area*

St. George Island is a small (20 km long x 8 km wide), irregular-shaped island located in the southeastern Bering Sea (56° 35' N 169° 35' W). Low cliffs of basalt comprise most of its perimeter; however, cliffs rise to an elevation of 300 m ASL in the northwestern corner of the island (Figure 1.1).

### *Whole-island Census*

I conducted a whole-island census of kittiwakes on St. George Island in 1995 using procedures similar to those employed by Hickey and Craighead (1977). In 1976, Hickey and Craighead (1977) photographed the cliffs around the entire perimeter of the island from an inflatable boat using a Pentax 6x7 camera, a 105 mm lens, and Tri-X, black and white film. An initial set of whole-island photographs was taken on 7 July and 15 July, a second set was taken 29 July, and additional photographs of high-elevation areas in the northwestern corner of the island were taken 5-6 August. Most photographs that were later used for census purposes were taken on 29 July, a date corresponding to the peak-hatch period of kittiwakes in 1976 (mean hatch date for Red-legged Kittiwakes = 5 Aug and for Black-legged Kittiwakes = 28 July; Dragoo and Dragoo 1996).

Hickey and Craighead (1977) determined the number of kittiwakes on St. George Island by counting all "white birds" within the boundaries of 100, 30 m x 30 m "random" plots (that were randomly located on 11" x 14" enlargements of whole-island photographs) and partitioning white-bird counts into Red-legged Kittiwake, Black-legged

Kittiwake, and Northern Fulmar (*Fulmaris glacialis*) fractions using the relative abundances of these species from single counts of 63 land-based plots located around the perimeter of the island. They estimated whole-island population totals by multiplying average bird densities determined from "random" plots by an estimate of the total surface area of cliffs on St. George Island.

In 1995 I censused kittiwakes on St. George Island by photographing cliffs around the entire perimeter of the island from a Zodiac boat and counting kittiwakes directly from photographic negatives using a dissecting microscope. Photographs were taken within daily and seasonal census windows that were established by the USFWS for land-based census work on St. George Island (Byrd et al. 1985, Byrd 1989) to minimize effects of daily and seasonal variability in the colony attendance of kittiwakes on St. George Island: cliffs were photographed within a daily census window between 1200-2000 hrs ADT (Alaska Daylight Time = GMT - 8 hrs; solar noon on St. George Island = 1520 hrs ADT) and within a seasonal census window between the last day of egg laying (9 July) and first day of fledging (5 August) of Thick-billed Murres (*Uria lomvia*)(Dragoo and Dragoo 1996). Photographing cliffs from a small boat required weather conditions that are exceptionally rare on St. George Island: no fog, calm seas, and a cloud ceiling greater than 300 m. In 1995, I photographed most of the perimeter of the island on two days, 27 July and 30 July, approximately 2 weeks after the mean hatch date of 12 July for Red-legged Kittiwakes (Dragoo and Dragoo 1996), and near the end of the seasonal census window for that year.

Photographs were taken with a Pentax 6x7 medium format camera and a 300 mm lens. I exposed 55 rolls of 400 ASA Kodak PMC color print film at a maximum aperture setting of *f* 4.5 and a minimum shutter speed of 1/1000th of a second. With these camera settings and the overcast conditions prevalent on St. George Island during the summer months, photographs were underexposed by 1-2 *f*-stops. I did not reduce the shutter speed to correct the exposure because a fast shutter was required to "freeze" hand-held photographs on an unstable photographic platform. Cliffs were photographed at a

distance of 300 m (measured with a Ranging 1000 range finder) and each photograph covered an area of approximately 90 m x 90 m. The higher cliffs of St. George Island were photographed in three "tiers" that covered approximately 0 - 90 m, 90 - 180 m, and > 180 m in elevation ASL.

I overlapped 825 photographs in both horizontal and vertical directions, and delimited census boundaries on each, to produce a photographic map of the cliffs of St. George Island that was composed of 854 census areas. Two major gaps in photo coverage (10 and 6 photos wide, respectively) occurred because incorrect camera settings generated poor images. I filled in these gaps with the average count of an equivalent surface area of cliff from either side of the gap. Some sections of cliff could not be photographed from the water because they faced inland or occurred in narrow indentations. I did not attempt to compensate for these missed areas but subjectively estimated that they comprised no more than 3% of the total cliff area. In other instances, slivers of cliff were not included in the photographic map because adjacent photos failed to overlap fully. I did not compensate for these missed areas because they accounted for less than 1% of the total cliff area.

Approximately 20% of the photographs were not clear enough to readily distinguish among kittiwakes, northern fulmars, and murres (*Uria* spp.). Although the photos appeared clear to the naked eye, the negatives were slightly out of focus and blurred when viewed at 10x magnification. I distinguished kittiwakes from murres in blurred photographs using the shape and posture of the bird: the white ellipse of the ventrum of a standing murre was elongated and oriented nearly vertically while the white ellipse of a kittiwake was more rounded and usually inclined at an angle of 45% or greater. I distinguished kittiwakes from fulmars on blurred photographs in two ways: 1) for upper tier photographs I classified all unidentifiable birds as kittiwakes because the relative abundance of kittiwakes and fulmars on clear upper tier photographs was 33:1 (Appendix A), and 2) for photographs within lower and middle tiers I used contextual cues to distinguish kittiwakes from fulmars: fulmars generally occur in uniformly spaced

strips of birds, are usually highlighted against a dark background, and are commonly found along interfaces between horizontal layers of basalt, in small caves, or on vegetated areas of cliff. In contrast, kittiwakes nest in loose clusters on rock cliff faces that present a more uniform background (pers. obs.).

I counted kittiwakes and fulmars directly from photographic negatives with the aid of a 7x - 30x dissecting microscope. Negative strips were mounted between two plates of 3 mm window glass and were illuminated from below with a microscope light. With this equipment I was able to regulate both magnification and light intensity when counting negatives and could standardize the brightness of the image and the size of birds in the field of view. Most negatives were counted at magnifications of between 8x and 10x.

I counted the number of kittiwakes and fulmars present within the defined census boundaries of each photograph and recorded the following: the date and time at which the photograph was taken, the elevational tier and cliff section of the photograph (Figure 1.1), and the clarity of the photograph (sharp = perfectly focused, good = kittiwakes, fulmars and murres can be distinguished directly, blurred = contextual cues needed to distinguish birds). Raw counts of whole-island census photographs are presented in Appendix A.

Raw counts are biased because I could not detect all kittiwakes present in photos and I misidentified some kittiwakes as fulmars and vice-versa. I corrected these biases by applying observability and misidentification correction factors (determined by comparing counts of census photos with counts of 24 close-up photographs of these same areas) to raw counts of photographs. To generate correction factors, I assumed that I could correctly identify all kittiwakes on close-up photographs and compared, bird for bird, these classifications with those made on standard census photos. I applied correction factors to raw census counts by assuming that the number of missed or mis-classified birds was proportional to the total number of kittiwakes and fulmars in the photograph. I computed two correction factors and their variances using a cluster sampling procedure

for proportions (Scheaffer et al. 1986): 1) the proportion of kittiwakes missed or misidentified as fulmars in standard census photographs, and 2) the proportion of fulmars misclassified as kittiwakes in standard census photographs. I computed separate correction factors for sharp and good quality ground-truthed photographs (Table 1.1) and applied sharp correction factors to raw counts of sharp census photographs and good correction factors to raw counts of both good and blurred census photographs (see Table 1.1 for an example). For each photograph, I determined the variance of the corrected count using the delta method (Seber 1982). I then pooled census photographs within each elevational tier of 10 cliff sections (indicated in Figure 1.1) and totaled adjusted kittiwake counts and their variances within each subsection of cliff (Table 1.2).

I could not distinguish between Red-legged and Black-legged Kittiwakes on census photos. To partition total kittiwake counts for each subsection of cliff (each tier within each cliff section) into Red-legged and Black-legged Kittiwake fractions, I used the relative abundance of the two species observed on land-based reference plots located within each subsection. I censused adult Red-legged and Black-legged Kittiwakes on 54 land-based plots between 19 July and 5 August 1995 (see "Land-Based Counts" section for details) and used means of counts of Red-legged and Black-legged Kittiwakes on each plot for reference purposes. In addition, I monitored the number of nest attempts of each species of kittiwake on 372 nest-mapping plots during early, and late-incubation visits to plots in the 1993-1995 breeding seasons and used species totals from these plots for reference purposes. Nest-mapping plots were distributed across most subsections of cliff on St. George Island; however, where fewer than 100 birds or nests were monitored within a given subsection, I pooled data from adjacent subsections of cliff (Table 1.3). I used nest-mapping data from 1994 for reference purposes because in 1995 both kittiwake species had poor reproductive success on St. George Island (Dragoo and Dragoo 1996), and nest counts did not reflect the relative abundance of adults of each species present. I determined the mean proportion of Red-legged and Black-legged Kittiwakes and its variance within each subsection of cliff (Table 1.3) using a cluster sampling procedure for

proportions (Scheaffer et al. 1986) and partitioned adjusted counts into Red-legged and Black-legged Kittiwake fractions (Table 1.2). I determined the variance of the product of adjusted census counts (Y) and species proportions ( Z) using an equation that assumes independence of random variables Y and Z (Mood et al. 1974):

$$var[YZ] = (Y^2)(var[Z]) + (Z^2)(var[Y]) + (var[Y])(var[Z])$$

If the two variables are correlated, then the variance of the product is best determined using a boot-strap procedure (Efron 1982). Although I lack the appropriate data to test the assumption of independence, I used the above equation to calculate the variance because I had no *a priori* expectation that adjusted count totals and species proportions would be correlated across years. I generated whole-island population estimates for each species of kittiwake by pooling species totals and their variances across the 16 subsections of cliff (Table 1.2).

Lastly, I determined the density of kittiwakes within each elevational tier (Table 1.4) by dividing the total number of each species within each tier by estimates of the surface area of each tier (determined by measuring the length and elevation of cliffs on a detailed topographic map of St. George Island).

*Land-based Counts*

Over the past 20 years, kittiwake numbers on St. George Island have been monitored on land-based plots that were initially established in 1976 by Hickey and Craighead (1977). Counts were made in 1982 (Craighead and Oppenheim 1985), 1984 (Troy and Baker 1985), and 1985 - 89 and 1992 (USFWS; summarized in Dragoo and Sundseth 1993). I censused adult kittiwakes on these same plots in 1995 using census procedures established by the USFWS in 1985 (Byrd et al. 1985). In 1995, most counts of adult kittiwakes and nests were conducted within a daily census window of 1200-2000 hrs (ADT) and between 19 July and 5 August, a time period falling within a seasonal census window defined by the first hatching (9 July) and first fledging (5 August) of Thick-billed Murre chicks (Dragoo and Dragoo 1996). I departed from the USFWS

census protocol by counting each plot only once on each visit instead of 2 or more times on each visit. I censused kittiwakes at a total of 54 plots (Appendix B) and, with the exception of four plots within the Red Bluff section of cliff which were counted only once, obtained a minimum of two replicate counts for each of 51 "common" census plots on St. George Island. Common plots are a sub-sample of census plots for which data have been collected in every census year since 1976 (see Dragoo and Sundseth 1993).

*Census Trends*

I did not statistically compare whole-island census totals between 1995 and 1976 because census methods differed markedly between years and both censuses were unreplicated. Prior to graphically comparing whole-island census totals between 1976 and 1995, I corrected biases and mathematical errors present in the original 1976 census totals. Hickey and Craighead (1977) determined whole-island totals by multiplying estimates of kittiwake density determined from 100 random plots (each 30 m x 30 m) by an estimate of the surface area of all cliffs on St. George Island. In the original report, a computational error in table underestimated the whole-island total of the number of Red-legged Kittiwakes by 12,372 individuals: the estimate of Red-legged Kittiwake density for "stratum 2" in table 22, when multiplied by the area estimate for stratum 2 in table 26, does not equal the total reported in table 26 (Hickey and Craighead 1977). In addition, estimates of cliff area used in the original report to calculate whole-island population totals were imprecise (Table 1.5). Hickey and Craighead (1977) divided the cliffs into 5 elevational strata (each 61 m thick) and determined the total surface area of each by multiplying the cumulative length of each stratum by an arbitrary estimate of its thickness (30.5 m for most strata). I used actual measurements of the length and thickness of strata that were determined from a detailed topographic map of St. George Island to calculate the cliff area of each stratum and recalculated whole-island census totals for each species of kittiwake (Table 1.5). Lastly, for these calculations I used corrected estimates of the density of both Red-legged and Black-legged Kittiwakes within the two highest elevation

strata on St. George Island. Hickey and Craighead (1977) assumed that the relative magnification of birds in census photographs was uniform across elevation when, in fact, magnification diminishes at higher elevations because the cliff-camera distance is greater. In the original report, the density of kittiwakes was overestimated by a factor of 2.3 within stratum 5 and by a factor of 1.6 within stratum 4 (Figure 1.2). Using corrected estimates of cliff area and kittiwake density, I generated corrected census totals of 168,368 Red-legged Kittiwakes and 81,543 Black-legged Kittiwakes for 1976 (Table 1.5).

I statistically evaluated trends in land-based census counts between 1976 and 1995 by fitting linear and quadratic regression models to census data for each kittiwake species. I determined annual census totals for each kittiwake species for 10 census years by summing mean counts of kittiwakes on 50 common census plots within each year. In computing annual census totals, I excluded data from plot #33 (one of 51 common plots on St. George Island) because a significant portion of the census face had eroded away during the 1980's and was no longer visible from the observation point.

*Censusing Kittiwakes from Photographs*

In 1995, I evaluated the reliability of censusing kittiwakes on land-based plot from photographs, rather than direct counts, by photographing 8 census plots at high elevation using a Pentax K1000 camera, a 60-300 mm lens, and Kodachrome, color slide film (200 ASA) immediately before conducting direct counts of kittiwakes on those plots. I compared direct counts and counts from photographs with a paired-sample t-test.

## RESULTS

*Whole-island Census*

Raw counts of kittiwakes on photographs of the cliffs of St. George Island in 1995 (Appendix A) totaled 183,261 birds (Table 1.2). When I adjusted raw counts for observability bias (Table 1.1), counts totaled 202,874 ± 369 (95% CI) kittiwakes (Table

1.2). I partitioned this adjusted total between kittiwake species (Table 1.3) to generate census totals of 156,902 ± 3793 (95% CI) Red-legged Kittiwakes and 45,972 ± 3780 (95% CI) Black-legged Kittiwakes (Table 1.2). The 95% confidence intervals associated with these census totals only reflect variability associated with the correction factors that were applied to raw counts. Census totals are unreplicated point estimates because they were not derived from a "sample" of whole-island counts and, hence, incorporate no within-year measure of temporal variability in kittiwake numbers. In contrast, counts of land-based census plots on St. George Island were replicated in 1995 and had coefficients of variation (= CV = standard deviation / mean) of 5.0% for Red-legged Kittiwakes and 7.7% for Black-legged Kittiwakes, values that were comparable to CVs for temporally-replicated, land-based counts of kittiwakes in 6 other census years on St. George Island (mean CV = 7.7% for both species of kittiwake; Dragoo and Sundseth 1993). If the temporal variability in whole-island counts of kittiwakes was no greater than that observed in land-based counts, then, assuming normality, the 95% confidence interval would have been no greater than ± 15.4 % of the whole-island census total. I added this source of variability to whole-island estimates for kittiwakes in 1995 and produced census totals of 156,902 ± 27,956 (95% CI) Red-legged Kittiwakes and 45,972 ± 10,860 (95% CI) Black-legged Kittiwakes.

Both the density and relative abundance of Red-legged Kittiwakes increased markedly with elevation on St. George Island (Table 1.4). Within the lowest elevational tier, the population density of Red-legged and Black-legged Kittiwakes was similar (approx. 100 birds / ha); however, within the highest elevational tier, the density of Red-legged Kittiwakes was 18 times greater than at low elevation and Red-legged Kittiwakes outnumbered Black-legged Kittiwakes 22:1 (Table 1.4). Approximately 40% of the Red-legged Kittiwake population on St. George Island occurred at high elevation, within a section of cliff that comprised less than 7% of the total cliff area of the island. In contrast, Black-legged Kittiwakes were more uniformly distributed across elevations on St. George Island (Table 1.4).

*Land-based Counts*

Counts of 51 land-based, "common" plots in 1995 (Appendix B) totaled 2,480 Red-legged Kittiwakes and 694 Black-legged Kittiwakes. When I excluded data from census plot #33, counts for the remaining 50 census plots totaled 2,404 Red-legged Kittiwakes and 675 Black-legged Kittiwakes and were the highest recorded since the mid-1980's for both species on St. George Island (Figure 1.3).

*Census Trends*

Whole-island census totals for Red-legged and Black-legged Kittiwakes in 1995 were 93 % and 56 % of corrected whole-island totals for 1976, respectively (Figure 1.4). In comparison, count totals for the land-based census in 1995 were 70 % and 77 % of counts in 1976 for Red-legged and Black-legged Kittiwakes, respectively (Figure 1.4). I statistically evaluated trends in land-based census counts over the past 20 years with linear and quadratic regressions. Linear models fit moderately well for Red-legged Kittiwakes (census total = 8585 - 71.7(year); n = 10, $r^2$ = 0.57) but poorly for Black-legged Kittiwakes (census total = 1548 - 11.0(year); n = 10, $r^2$ = 0.23). Quadratic models fit data better for both Red-legged Kittiwakes (census total = 1760 - 37.5(year-1900) + 0.207(year-1900)$^2$; n = 10, $r^2$ = 0.83) and Black-legged Kittiwakes (census total = 2421 - 53.9(year-1900) + 0.307(year-1900)$^2$; n = 10, $r^2$ = 0.89)(Figure 1.3).

*Censusing Kittiwakes from Photographs*

To determine the efficacy of conducting kittiwakes censuses from photographs, I compared direct counts of kittiwakes on land-based census plots with counts determined from photographs. Although, on average, photo counts were1.7% lower than direct counts, they did not differ statistically ($t_{7\,df}$ = 1.72, p = 0.14).

# DISCUSSION

*Whole-Island Census*

The whole-island census of kittiwakes on St. George Island in 1995 produced estimates of 156,902 ± 27,956 (95% CI) Red-legged Kittiwakes and 45,972 ±10,860 (95% CI) Black-legged Kittiwakes. Census totals are not direct measures of the size of kittiwake populations that are associated with St. George Island during the breeding season, rather, they are measures of the cliff attendance of kittiwake populations during the census period. Moreover, they are minimum estimates only because some cliff area was not covered by census photos, and observability correction factors likely underestimated the number of kittiwakes missed on higher-elevation cliff faces, in blurred photos, and on cliff faces that could not be photographed straight-on.

I revised the global estimate of the breeding population of Red-legged Kittiwakes using data from my whole-island census of this species on St. George Island and data from recent whole-island censuses of Red-legged Kittiwakes at other breeding colonies (Byrd et al. 1997). At all other colonies, the breeding population of Red-legged Kittiwakes was determined by doubling whole-island counts of Red-legged Kittiwake nests. To make my census of the colony attendance of Red-legged Kittiwakes comparable to nest censuses conducted at other colonies, I multiplied my whole-island total by the average ratio of nests / birds observed on land-based census plots on St. George Island. To perform this calculation, I did not use the nest / bird ratio for Red-legged Kittiwakes in 1995 because 1995 was a year of poor reproductive performance (< 0.15 fledged chicks / nest attempt), and few kittiwakes maintained their nests through the census period. Instead, I used the average nest / adult ratio from recent land-based censuses (< 10 years old) that were conducted in years when Red-legged Kittiwakes exhibited at least moderate reproductive performance on St. George Island (> 0.15 chicks fledged / nest attempt; Dragoo and Sundseth 1993). I multiplied the whole-island count of Red-legged Kittiwakes (156,902 individuals) by this composite nest / adult ratio (0.618) and estimated that the breeding population of Red-legged Kittiwakes on St.

George Island (96,965 nests = 193,930 individuals) comprises 81% of the global breeding population of this species (239,060 individuals; Table 1.6). Similarly, I determined an estimate of the breeding population of Black-legged Kittiwakes on St. George Island (31,284 nests = 62,568 individuals) by multiplying the whole-island count of Black-legged Kittiwakes (65,972 individuals) by the composite nest / adult ratio (0.680) of this species.

The density and relative abundance of Red-legged and Black-legged Kittiwakes differed markedly between high- and low-elevation areas on St. George Island in both 1976 and 1995. Although both species nested in approximately equal numbers at lower elevations, the density of Red-legged Kittiwakes was more than an order of magnitude greater at higher elevations (Table 1.4). Currently, the reason for the exceptional abundance of Red-legged Kittiwakes at higher elevations on St. George Island is not clear; however, Kildaw (in press) speculates that it has arisen because of differences in nesting substrate between high- and low-elevation areas and differences in the nest-site preferences of Red-legged and Black-legged Kittiwakes.

*Census Trends*

Relative to corrected census totals for 1976, whole-island census totals for Red-legged and Black-legged Kittiwakes in 1995 were 93 % and 56 % of their former levels, respectively (Figure 1.4). Comparisons between years should be interpreted with caution because census methods differed markedly: census totals for 1976 are crude estimates because random plots represented only 2.5% of the total cliff area and only 10 random plots were located within the two highest-elevation strata where Red-legged Kittiwakes nest at extremely high densities (Hickey and Craighead 1977). In particular, the corrected 1976 census total (Table 1.5) underestimated the number of Red-legged Kittiwakes on St. George Island because "white birds" were difficult to identify (and count) in photographs of high-elevation cliffs (pers. obs.) where Red-legged Kittiwakes were concentrated. In contrast, the corrected 1976 census total for Black-legged Kittiwakes is likely a better

estimate because "white birds" were readily identified in photographs of lower-elevation cliffs where the bulk of the Black-legged Kittiwake population on St. George Island was located (Hickey and Craighead 1977).

Land-based census counts in 1995 on St. George Island were the highest recorded since the early-1980's for both kittiwake species (Figure 1.3). The superior fit of quadratic vs. linear regression models to data from land-based censuses suggests that census trends were not monotonic for either kittiwake species. Counts of both species declined by approximately 40 % between 1976 and the late-1980's, but have stabilized since then.

Trends in whole-island and land-based censuses should be interpreted with caution because attendance counts are not a direct measure of population size and variation in attendance has been documented at within-day (Byrd 1989, Hickey and Craighead 1977, Troy and Baker 1985), within-season (Troy and Baker 1985), and inter-annual time scales (Hatch and Hatch 1988, Murphy et al. 1991). Although census protocols established by the USFWS for St. George Island restrict counts to time periods when both within-day and among-day variation in kittiwake attendance is minimized, attendance is sensitive to a number of factors that cannot be controlled (e.g. reproductive performance, weather) and which may vary independent of the size of the breeding population. Furthermore, census counts are also affected by the number of subadult birds in adult plumage, and factors that influence the proportion of the breeding population that make no attempt to breed in a given year.

Kittiwake attendance may have differed among census years because the reproductive performance of kittiwakes has been highly variable over the past 20 year (Dragoo and Dragoo 1996): kittiwakes may exhibit reduced and highly variable attendance in the late incubation stage of the breeding cycle in years of reproductive failure (Murphy et al. 1991) because the activity patterns of kittiwakes with active nests differ from that of failed breeders (Hatch and Hatch 1988). Kittiwake attendance may have also differed among census years because the breeding chronology of kittiwakes has

advanced by three weeks relative to the timing of census counts (Figure 1.5). If there is a consistent seasonal trend in kittiwake attendance on St. George Island, then the advancement of the relative timing of kittiwake censuses could generate a spurious trend in whole-island and land-based censuses. Although there were insufficient data to statistically evaluate seasonal trends in census counts, census data from replicated land-based plots on St. George Island do not suggest a consistent seasonal trend for either species over the past 20 years (Figures 1.6, 1.7).

Evidence for population declines of kittiwakes on St. George Island is largely dependent on unreplicated land-based census counts that were conducted in 1976; however, I argue that the 40 % reduction in kittiwake counts between 1976 and the mid 1980's could not have been an artifact of the lack of replication of the land-based census in 1976. To begin with, effects of among-day variability in nest attendance on census totals was dampened because, though unreplicated, counts of different plots were distributed over several different days. Furthermore, the average CV of counts of Red-legged Kittiwakes (8.3 %) and Black-legged Kittiwakes (12 %) for 2 land-based census plots that were replicated in 1976 (Figure 1.8; J. Hickey, unpublished data) was comparable to the average CV of replicated counts for land-based plots in other years (7.7 %). A CV of 7.7 correspond to a 95 % confidence interval of 15.4 %, a figure that is less than half the magnitude of the decline observed between 1976 and the late-1980's. Finally, replicated counts of 2 census plots in both 1975 and 1976 further suggest that kittiwake numbers in 1976 were not artificially inflated: counts were similar between years (Figure 1.8; J. Hickey, unpublished data).

*Censusing Kittiwakes from Photographs*

The greatest limitation to census work on St. George Island is the unpredictability of the weather. On any given day, dense fog can abruptly terminate census work in mid-count, particularly at higher elevation areas of the island that are critical census areas for Red-legged Kittiwakes. Censusing kittiwakes from photographs would make the most of

ephemeral windows of favorable weather conditions because photographing census plots requires only a fraction of the amount of time needed to conduct direct counts of kittiwakes in the field. I found negligible difference between direct counts of kittiwakes on land-based census plots and counts determined from photographs; thus, I conclude that a photographic approach is a time-efficient back-up method for censusing kittiwakes on St. George Island.

*Recommendations for Future Censuses*

I recommend the following modifications for future whole-island censuses of kittiwakes on St. George Island: a) be obsessive about the sharpness of focus when using a Pentax 6x7 camera with a 300 mm lens and maximum aperture setting, because the depth of field is extremely shallow; b) use slower film (200 ASA), a shutter speed of 1/500th of a second, and a shorter lens (200 mm) to take photographs that each cover an area of roughly 150 m x 150 m: this revised census protocol would reduce the number of photographs needed to cover the island and the amount of time needed to overlap and mark census boundaries on photographs without appreciably reducing the resolution of photographs; c) better standardize the boat-cliff distance by using a more accurate range finder; and d) replicate photographs of a sample of cliff around the perimeter of the island to determine a measure of temporal variability in kittiwake attendance that could be applied to whole-island population totals.

For land-based census work I recommend that a photographic census be integrated with the conventional direct census of high-elevation plots. When a window of visibility opens at high elevation, the fastest hiker of the census crew should initially photograph all census plots at high-elevation and at the same time count the relatively few Black-legged Kittiwakes on those plots. In the event that the window of visibility closes before direct counts can be made, a census of kittiwakes could thereby be completed from photographs. At present, data needed to evaluate the interactive effects of reproductive performance and census timing on patterns of kittiwake attendance are

lacking. To better interpret the trends in kittiwake populations on St. George Island that have occurred over the past 20 years requires data from many years in which kittiwake counts are replicated over a broad seasonal window. I recommend that these data be collected each year on St. George Island as part of the standard field procedures.

For both whole-island and land-based censuses I recommend that the timing of murre and kittiwake censuses be uncoupled in years when the breeding chronology of kittiwakes is exceptionally early (mean hatch date < July 15). Although no consistent seasonal trend in kittiwake attendance was observed in replicated census data for the past 20 years, kittiwake censuses should not be conducted beyond 14 days of the mean date of hatch to better standardize the relative timing of censuses.

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## LITERATURE CITED

Byrd, G.V. (1989) Seabirds of the Pribilof Islands, Alaska: trends and monitoring methods. Unpublished M.S. Thesis. University of Idaho, Moscow, Idaho, USA.

Byrd, G. V., Sievert, P. R. and Slater, L. (1985) Population trends and productivity of fulmars, cormorants, kittiwakes and murres in the Pribilof Islands, Alaska in

1985. U. S. Fish and Wildlife Service, Homer, Alaska, USA.

Byrd, G. V., Williams, J. C., Artukhin, Y.B., and Vyatkin, P.S. (1997) Trends in populations of Red-legged Kittiwake (*Rissa brevirostris*), a Bering Sea endemic. Bird Conservation International. 7:167-180.

Climo, L. (1993) The status of cliff-nesting seabirds at St. Paul Island, Alaska in 1992. Unpublished report. U. S. Fish and Wildlife Service, Homer, Alaska, USA.

Craighead, F. L., and Oppenheim, J. (1985) Population estimates and temporal trends of Pribilof Island seabirds. U. S. Department of Commerce, NOAA, OCSEAP. Final report 30:307-356.

Dragoo, D. E., and Dragoo, B. K. (1996) Results of productivity monitoring of kittiwakes and murres at St. George Island, Alaska, in 1995. U. S. Fish and Wildlife Service, Homer, Alaska, USA.

Dragoo, B. K., and Sundseth, K. (1993) The status of northern fulmars, kittiwakes, and murres at St. George Island, Alaska, in 1992. Unpublished report. U. S. Fish and Wildlife Service, Homer, Alaska, USA.

Efron, B. (1982) The jackknife, the bootstrap and other resampling plans. CBMS Regional Conference Series in Applied Mathematics 27, Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.

Hatch, S. A., and Hatch, M. A. (1988) Colony attendance and population monitoring of Black-legged Kittiwakes on the Semidi Islands. Condor 90:613-620.

Hickey, J. J., and Craighead, F. L. (1977) A census of seabirds on the Pribilof Islands. U.S. Department of Commerce, NOAA, OCSEAP, Boulder, Colorado, USA. Annual Reports of the Principal Investigators for the year ending March, 1977. 2:96-195.

Hunt, G. L. (1977) Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands. U. S. department of Commerce, NOAA, OCSEAP, Boulder, Colorado, USA. Annual Reports of the Principal Investigators for the year ending March, 1977. 2:196-382.

Johnson, S. R., and Baker, J. S. (1985) Productivity studies. Pages 191-256 *in* S. R. Johnson, ed. Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, Bering Sea, Alaska. LGL Ecological Research Associates, Inc., Bryant, Texas, USA.

Kildaw, S. D. In press. Competitive displacement? An experimental assessment of nest-site preferences of cliff-nesting gulls. Ecology.

Mood, A. M., Graybill, F. A., and Boes, D. C. (1974) Introduction to the theory of statistics. Third edition. McGraw-Hill, New York.

Murphy, E. C., Springer, A. M., and Roseneau, D. G. (1991) High annual variability in reproductive success of kittiwakes (*Rissa tridactlya* L.) at a colony in western Alaska. Journal of Animal Ecology (1991). 60:515-534.

Scheaffer, R. L., Mendenhall, W., and Ott L. (1986) Elementary survey sampling. Third edition. Prindle, Webber & Schmidt. Boston, MA.

Seber, G. A. F. (1982) The estimation of animal abundance. Alden press, Oxford, London.

Troy, D. M., and Baker, J. S. (1985) Population studies. Pages 34-190 *in* S. R. Johnson, ed. Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, Bering Sea, Alaska. LGL Ecological Research Associates, Inc., Bryant, Texas, USA.

Table 1.1. Correction factors for observability bias on whole-island census photos. Data for 24 close-up photos (see text).

| Census Photo | Photo Clairity | Truth Photo | Kittiwake Count (k) | Fulmar Count (f) | Missed Kittiwakes (x) | Fulmars Misidentified as Kittiwakes (fm) | Kittiwakes Misidentified as Fulmars (km) | Total Missed Kittiwakes (xkm) | Total Kittiwakes (K) | Total Fulmars (F) |
|---|---|---|---|---|---|---|---|---|---|---|
| m49-4 | sharp | c4-11 | 79 | 11 | 2 | 0 | 0 | 2 | 81 | 11 |
| m49-4 | sharp | c4-12 | 90 | 34 | 0 | 0 | 0 | 0 | 90 | 34 |
| m49-4 | sharp | c4-13 | 63 | 51 | 1 | 3 | 0 | 1 | 61 | 54 |
| m49-5 | sharp | c4-14 | 47 | 60 | 1 | 3 | 1 | 2 | 46 | 62 |
| m49-5 | sharp | c4-15 | 50 | 36 | 2 | 2 | 1 | 3 | 51 | 37 |
| m52-25 | sharp | m52-17 | 62 | 88 | 5 | 8 | 1 | 6 | 60 | 95 |
| m52-25 | sharp | m52-19 | 60 | 19 | 3 | 0 | 0 | 3 | 63 | 19 |
| m52-25 | sharp | m52-20 | 30 | 32 | 1 | 3 | 0 | 1 | 28 | 35 |
| | Totals for "Sharp" Photographs | | | | (n = 8) | $\overline{Tfm} = 19$ | | $\overline{Txkm} = 18$ | $\overline{TK} = 480$ | $\overline{TF} = 347$ |
| m42-2 | good | c4-0 | 29 | 12 | 7 | 0 | 0 | 7 | 36 | 12 |
| m42-2 | good | c4-1 | 21 | 44 | 1 | 0 | 0 | 1 | 22 | 44 |
| m42-2 | good | c4-2 | 21 | 53 | 2 | 0 | 0 | 2 | 23 | 53 |
| m42-2 | good | c4-3 | 0 | 31 | 1 | 3 | 0 | 1 | 1 | 34 |
| m42-2 | good | c4-4 | 1 | 20 | 2 | 2 | 0 | 2 | 3 | 22 |
| m42-2 | good | c4-5 | 21 | 28 | 8 | 1 | 1 | 9 | 29 | 28 |
| m42-2 | good | c4-6 | 42 | 53 | 4 | 4 | 0 | 4 | 42 | 57 |
| m42-2 | good | c4-7 | 6 | 42 | 1 | 0 | 0 | 1 | 7 | 42 |
| m49-7 | good | c4-22 | 151 | 63 | 19 | 5 | 2 | 21 | 167 | 66 |
| m49-7 | good | c4-23 | 98 | 35 | 9 | 1 | 1 | 10 | 107 | 35 |
| m49-7 | good | c4-24 | 153 | 22 | 24 | 0 | 1 | 25 | 178 | 21 |
| m52-21 | good | m52-11 | 23 | 22 | 4 | 4 | 0 | 4 | 23 | 26 |
| m52-21 | good | m52-13 | 66 | 102 | 4 | 1 | 1 | 5 | 70 | 102 |
| m52-22 | good | m52-14 | 58 | 79 | 2 | 4 | 0 | 2 | 56 | 83 |
| m52-22 | good | m52-15 | 61 | 60 | 10 | 2 | 0 | 10 | 69 | 62 |
| m52-22 | good | m52-16 | 29 | 69 | 1 | 4 | 0 | 1 | 26 | 73 |
| | Totals for "Good" Photographs | | | | (n = 16) | $\overline{Tfm} = 31$ | | $\overline{Txkm} = 105$ | $\overline{TK} = 859$ | $\overline{TF} = 760$ |

Correction factors were calculated seperately from the above data for "sharp" and "good" photographs using a cluster sampling procedure for proportions (Scheaffer et al. 1986):

$PK = Txkm / TK$ = propotion of mis-classified kittiwakes.
$PF = Tfm / TF$ = proportion of fulmars mis-classified as kittiwakes.

and:

$$\text{Vanance of } PK = VPK = (SE_{PK})^2 = (1 / (n (TK / n)^2)) (\Sigma (xkm - PK(K))^2 / (n - 1))$$
$$\text{Vanance of } PF = VPF = (SE_{PF})^2 = (1 / (n (TF / n)^2)) (\Sigma (fm - PF(F))^2 / (n - 1))$$

Raw kittiwake counts for whole-island census photographs (in Appendix A) were adjusted by the above correction factors using the following general equation:

$$Kc = Kr + (Kr(PK) / (1 - PK)) - (Fr(PF) / (1 - PF)) = \text{Adjusted kittiwake count}$$

where:

Kr = raw kittiwake count on census photograph (from Appendix A).
Fr = raw fulmar count on census photograph (from Appendix A).

and, using the "Delta Method" (Seber 1982):

$$\text{Variance of } Kc = (((Kr / (1 - PK)^2)^2) VPK) + (((Fr / (1 - PF)^2)^2) VPF)$$

Table 1.2. Raw counts from whole-island census photographs. Counts were pooled within 16 subsections of cliff (see Figure 1.1), adjusted for observability bias, then partitioned into Red-legged (RLKI) and Black-legged (BLKI) Kittiwake fractions using the proportion of each species within each section of cliff from Appendix C.

| Area | Tier[a] | n | Raw Count | Adjusted count | | RLKI | | BLKI | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Total | SE | Total | SE | Total | SE |
| Village | 1 | 60 | 2076 | 2331 | 6.5 | 896 | 119.1 | 1435 | 119.2 |
| First Bluff 211.3 | | 1 | 25 | 3937 | 4131 | 17.5 | 3123 | 211.6 | 1009 |
| | 2 | 13 | 2736 | 2839 | 13.2 | 2238 | 140.1 | 601 | 140.6 |
| High Bluff | 1 | 53 | 6629 | 7231 | 20.6 | 3792 | 407.7 | 3440 | 407.7 |
| | 2 | 69 | 29245 | 32493 | 64.5 | 27653 | 828.1 | 4841 | 826.3 |
| | 3 | 74 | 56421 | 63324 | 135.2 | 60530 | 568.8 | 2794 | 553.9 |
| Needle Rock | 1 | 52 | 12098 | 13364 | 32.5 | 5399 | 855.6 | 7966 | 855.7 |
| | 2 | 38 | 13906 | 15644 | 71.1 | 13961 | 452.1 | 1683 | 447.7 |
| Dalnoi | 1 | 26 | 2034 | 2248 | 9.1 | 1076 | 148.5 | 1172 | 148.5 |
| | 2 | 25 | 11248 | 12414 | 41.9 | 10772 | 274.6 | 1642 | 272.3 |
| Fox Castle | 1 | 49 | 3394 | 3662 | 13.8 | 1754 | 218.6 | 1909 | 218.7 |
| | 2 | 44 | 7681 | 8553 | 37.3 | 7182 | 298.4 | 1371 | 296.8 |
| Zapadni | 1 | 48 | 1292 | 1405 | 5.6 | 800 | 72.0 | 605 | 72.0 |
| Red Bluff | 1 | 99 | 12782 | 14053 | 31.4 | 8431 | 630.8 | 5623 | 630.7 |
| Garden Cove | 1 | 121 | 13594 | 14577 | 34.8 | 7494 | 873.3 | 7083 | 873.3 |
| Tolstoi | 1 | 58 | 4188 | 4600 | 15.2 | 1802 | 393.1 | 2798 | 393.2 |
| Whole-Island Totals | | | 183 261 | 202 875 | 188[b] | 156 902 | 1935[b] | 45 972 | 1929[b] |

[a] 1 = 0 - 91.5 m ASL, 2 = 91.5 - 183 m ASL, 3 = > 183 m ASL.

[b] Total SE = $(\Sigma SE^2)^{0.5}$

Table 1.3. Species composition of land-based census plots. Counts of adult kittiwakes on 54 land-based census plots and counts of kittiwake nests on 372 nest-mapping plots were used to determine the proportion of Red-legged (RLKI) and Black-legged (BLKI) Kittiwakes within 16 sections of cliff comprising the perimeter of St. George Island.

| | | Adult census data | | | Nest-mapping data | | | Pooled data | | Proportions | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | Tier | n | RLKI | BLKI | n | RLKI | BLKI | RLKI | BLKI | RLKI | BLKI | SE |
| Village | 1 | 3 | 566 | 1005 | 48 | 308 | 395 | 874 | 1400 | 0.384 | 0.616 | 0.051 |
| First Bluff | 1 | 1 | 34 | 14 | 11 | 144 | 44 | 178 | 58 | 0.756 | 0.244 | 0.051 |
| | 2 | 2 | 80 | 9 | 22 | 324 | 100 | 404 | 109 | 0.788 | 0.212 | 0.049 |
| High Bluff | 1 | - | - | - | - | - | - | 445[a] | 368[a] | 0.524 | 0.476 | 0.056 |
| | 2 | - | - | - | 1 | 18 | 10 | 1141[a] | 168[a] | 0.851 | 0.149 | 0.025 |
| | 3 | 7 | 1943 | 922 | 126 | 4443 | 203 | 6386 | 295 | 0.956 | 0.044 | 0.008 |
| Needle Rock | 1 | - | - | - | 19 | 183 | 270 | 183 | 270 | 0.404 | 0.596 | 0.064 |
| | 2 | - | - | - | 37 | 821 | 99 | 821 | 99 | 0.892 | 0.108 | 0.029 |
| Dalnoi | 1 | - | - | - | - | - | - | 289[b] | 278[b] | 0.479 | 0.521 | 0.066 |
| | 2 | - | - | - | - | - | - | 1461[b] | 221[b] | 0.868 | 0.132 | 0.022 |
| Fox Castle | 1 | - | - | - | 4 | 65 | 0 | 289[c] | 278[c] | 0.479 | 0.521 | 0.060 |
| | 2 | - | - | - | 41 | 681 | 130 | 681 | 130 | 0.840 | 0.160 | 0.035 |
| Zapadni | 1 | 14 | 41 | 4 | - | - | - | 457[d] | 401[d] | 0.570 | 0.430 | 0.051 |
| Red Bluff | 1 | 16 | 212 | 171 | 32 | 204 | 186 | 638[e] | 434[e] | 0.600 | 0.400 | 0.045 |
| | 2 | 2 | 27 | 9 | 17 | 195 | 68 | | | | | |
| Garden Cove | 1 | - | - | - | - | - | - | 884[f] | 868[f] | 0.514 | 0.486 | 0.060 |
| Tolstoi | 1 | 9 | 144 | 356 | 14 | 148 | 98 | 292 | 454 | 0.392 | 0.609 | 0.085 |

[a] Includes First Bluff and Needle Rock data.

[b] Includes Needle Rock and Fox Castle data.

[c] Includes Needle Rock and Zapadni data.

[d] Includes Red Bluff and Fox Castle data from.

[e] Teirs 1 and 2 pooled for census purposes.

[f] Includes Red Bluff and Tolstoi data.

Table 1.4. Elevational stratification of kittiwakes within St. George Island. The density of Red-legged (RLKI) and Black-legged (BLKI) Kittiwakes within 3 elevational tiers is presented for whole-island censuses in 1976 and 1995.

| Tier [a] | Area [b] (ha) | 1976 CENSUS | | | | 1995 CENSUS | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Count Totals [c] | | Density [c] (#/ha) | | Count Totals | | Density (#/ha) | |
| | | RLKI | BLKI | RLKI | BLKI | RLKI | BLKI | RLKI | BLKI |
| 1 | 278.9 | 65,430 | 68,270 | 239 | 241 | 34,567 | 33,039 | 124 | 118 |
| 2 | 94.2 | 66,767 | 10,718 | 709 | 114 | 61,805 | 10,139 | 556 | 108 |
| 3 | 26.6 | 38,032 | 2,735 | 1430 | 103 | 60,530 | 2,794 | 2277 | 105 |

[a] 1 = 0 - 91.5 m ASL, 2 = 91.5 - 183 m ASL, 3 = > 183 m ASL.

[b] Determined from distance and elevation measurements from a detailed topographic map of St. George Island.

[c] Computed from corrected census totals (see text) for 1976 (Table 1.5).

Table 1.5. Original and corrected whole-island census totals for kittiwakes on St. George Island in 1976. Original data for Red-legged (RLKI) and Black-legged (BLKI) Kittiwakes were obtained directly from Hickey and Craighead (1977). Corrected totals were calculated using cliff-area measurements that were determined from a detailed topographic map of St. George Island, and using kittiwakes densities that were adjusted to remove bias due to image compression in census photos of higher-elevation cliffs (see Fig. 1.2).

ORIGINAL CENSUS DATA FOR 1976

| Strata [a] | Length (km) | Width (m) | Area (ha) | Density (#/ha) | | Total | |
|---|---|---|---|---|---|---|---|
| | | | | RLKI | BLKI | RLKI | BLKI |
| 1 | 48.7 | 34.0 | 162.5 | 176.7 | 291.1 | 28,714 | 47,304 |
| 2 | 33.5 | 30.5 | 102.2 | 396.7 | 115.5 | 40,543[b] | 11,804 |
| 3 | 14.4 | 30.5 | 43.9 | 1078.8 | 112.2 | 47,359 | 4,926 |
| 4 | 5.3 | 61.0 | 32.3 | 1505.5 | 172.2 | 48,628 | 5,562 |
| 5 | 4.2 | 30.5 | 12.8 | 5450.0 | 147.7 | 69,760 | 1,891 |
| | | | | Original Whole-Island Totals | | 235,004[c] | 71,487[c] |

CORRECTED CENSUS DATA FOR 1976

| Strata [a] | Length (km) | Width (m) | Area [d] (ha) | Density (#/ha) | | Total | |
|---|---|---|---|---|---|---|---|
| | | | | RLKI | BLKI | RLKI | BLKI |
| 1 | 40.3 | 51.0 | 205.5 | 176.7 | 291.1 | 36,312 | 59,822 |
| 2 | 26.6 | 46.8 | 124.5 | 396.7 | 115.5 | 49,389 | 14,330 |
| 3 | 11.4 | 37.8 | 43.1 | 1078.8 | 112.2 | 47,496 | 4,836 |
| 4 | 3.6 | 54.2 | 19.5 | 940.9 | 107.6 | 18,348 | 2,099 |
| 5 | 2.8 | 25.4 | 7.1 | 2369.5 | 64.2 | 16,823 | 456 |
| | | | | Corrected Whole-Island Totals | | 168,368 | 81,543 |

[a] 1 = 0 - 61 m ASL, 2 = 61 - 122 m ASL, 3 = 122 - 183 m ASL, 4 = 183 - 244 m ASL, 5 > 244 m ASL.
[b] The original figure presented in Hickey and Craighead (1977), 28,148, was computed incorrectly (see text).
[c] Figures differ from those presented in Hickey and Craighead (1977) because of [b] and rounding differences.
[d] Area computed from distance and elevation measurements taken from a detailed topographic map of St. George Island.
[e] Kittiwake density corrected for image compression in higher-elevation census photos (see Fig. 1.2).

Table 1.6. An estimate of the global breeding population of Red-legged Kittiwakes.

| Colony | Estimated Breeding Population | Year of Estimate | Source |
|---|---|---|---|
| Pribilof Islands | | | |
| St. George Is. | 193,930 [a] | 1995 | This Study |
| St. Paul Is. | 782 [b] | 1992 | Hunt (1977), Climo (1993) |
| Otter Is. | 2,000 [c] | 1993 | Byrd et al. (1997) |
| Buldir Island | 9,350 [c] | 1993 | Byrd et al. (1997) |
| Bogoslof Islands | 654 [c] | 1993 | Byrd and Williams (1994) |
| Commander Islands | 32,344 [c] | 1993 | Byrd et al. (1997) |
| TOTAL POPULATION | 239,060 | | |

[a] Breeding population determined from a whole-island count of Red-legged Kittiwakes (156,902 individuals) that was converted to a nest-census equivalent by multiplying the total by the average ratio of nests/adults (0.618) observed in recent land-based censuses (see text).

[b] Breeding population determined by discounting a nest census (850 nests) that was conducted in 1976 ( Hunt 1977) by a 54% reduction in counts of kittiwakes that occurred between 1976 and 1992 on land-based census plots on St. Paul Island (Climo 1993).

[c] Breeding population determined by multiplying a whole-island nest count by 2.

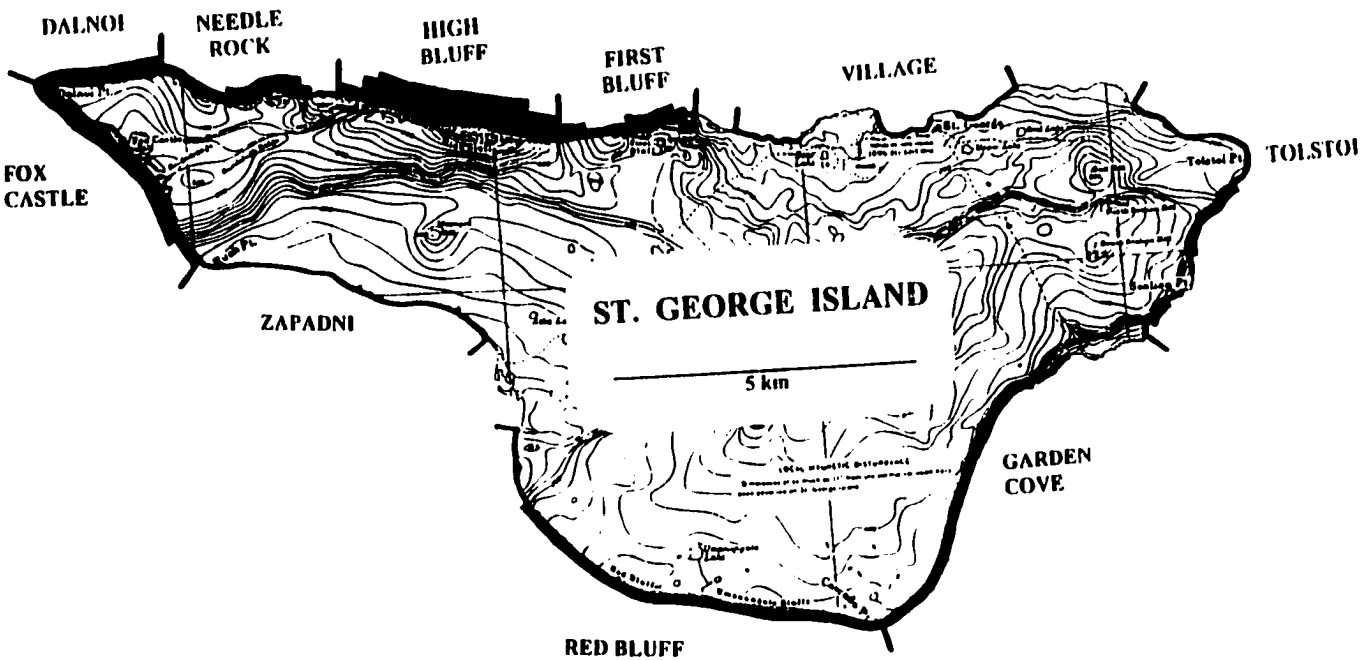


Figure 1.1. Cliff sections delineated on St. George Island, Alaska. The relative thickness of the black bar around the perimeter of the island corresponds to cliff height (in 61 m increments).

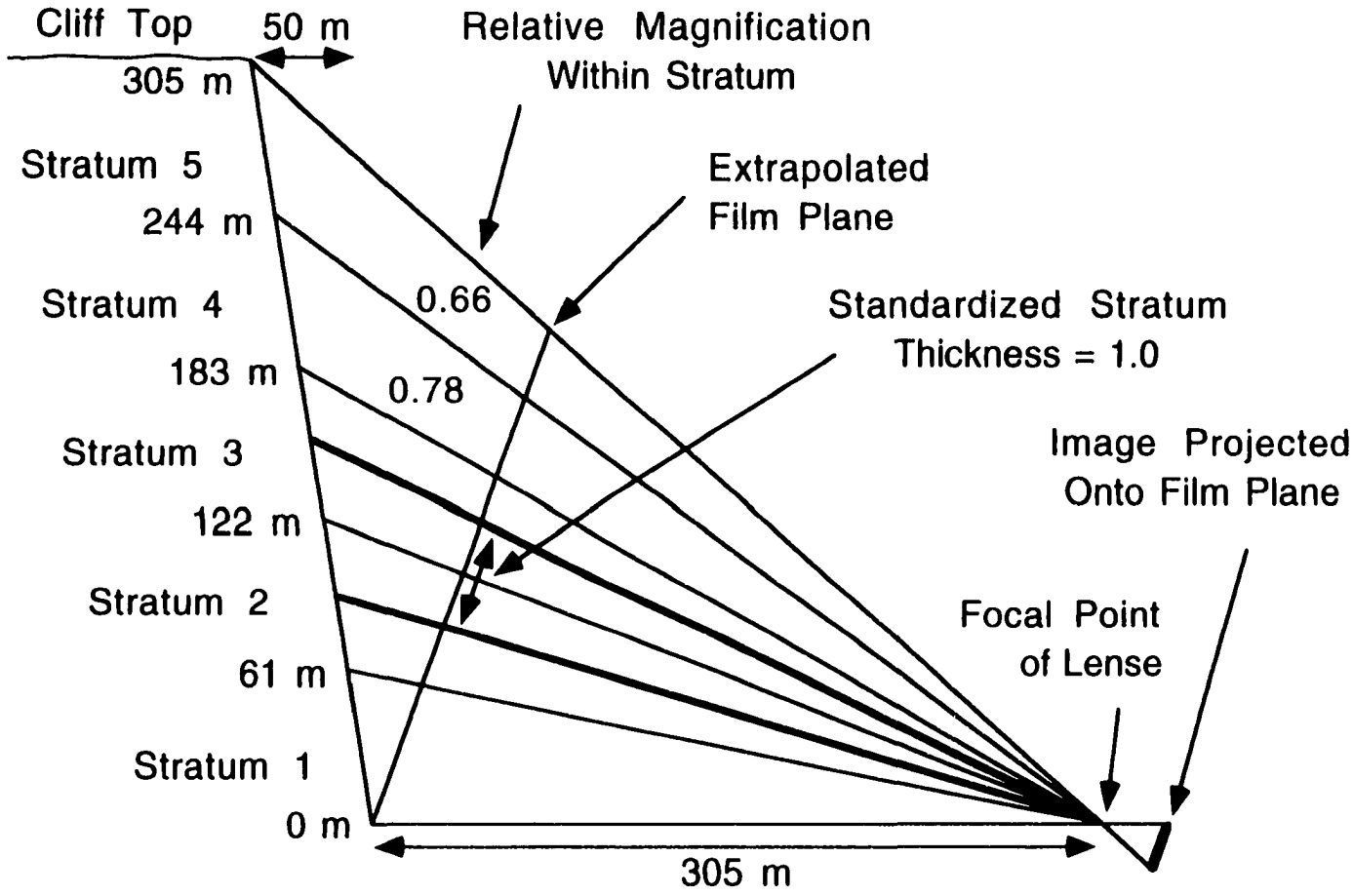


Figure 1.2. Image compression in photos of high-elevation cliffs. Boat distance and cliff height estimated to be 305 m, with the cliff top displaced 50 m back from vertical. Relative Magnification determined by comparing distance occupied on the projected film plane against a centrally located standardized stratum. Correction factors applied to bird densities were computed by squaring apparent stratum thickness to convert it from a linear measurement to a two-dimensional surface area measurment.

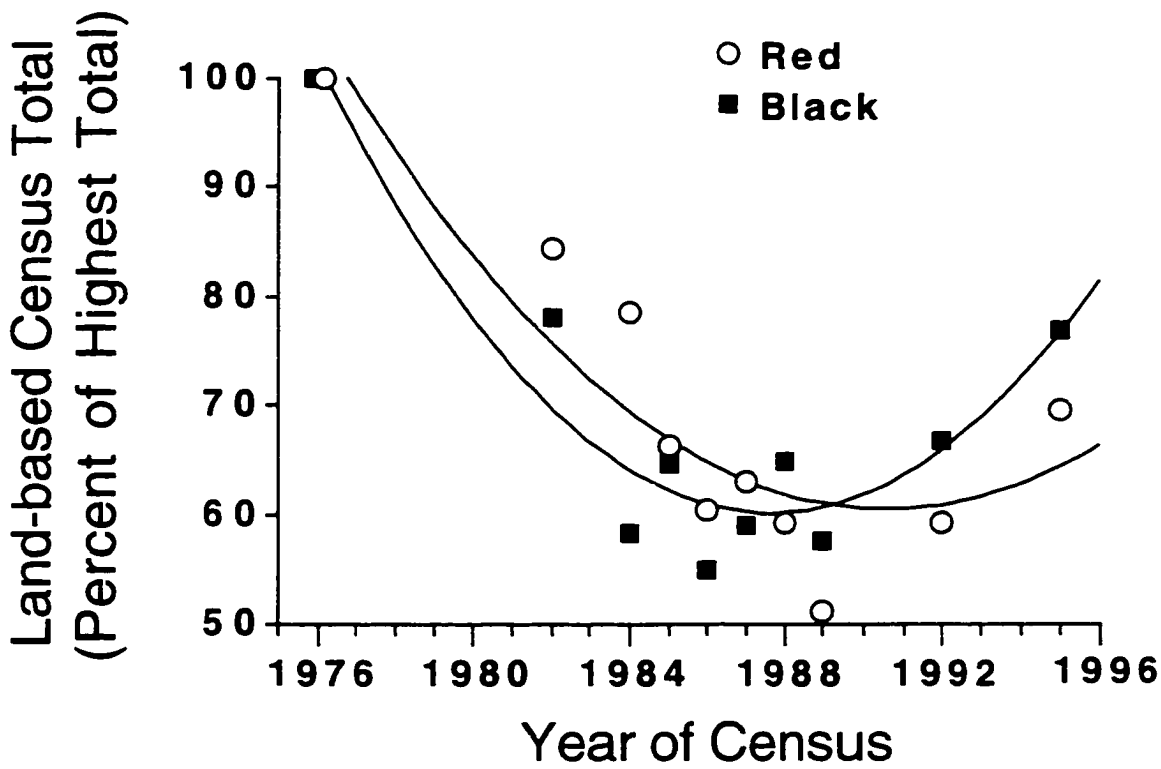


Figure 1.3. Population trends of kittiwakes on St. George Island. Counts of Red-legged (Red) and Black-legged (Black) kittiwakes on 50 land-based census plots (plot #33 excluded, see text) presented as a percentage of the 1976 total. Quadratic regression lines are shown. Data from the following sources: 1976, Hickey and Craighead (1977); 1982, Craighead and Oppenheim (1985); 1984, Troy and Baker (1985); 1985-1992, Dragoo and Sundseth (1993); and Alaska Maritime National Wildlife Refuge (unpulished data).

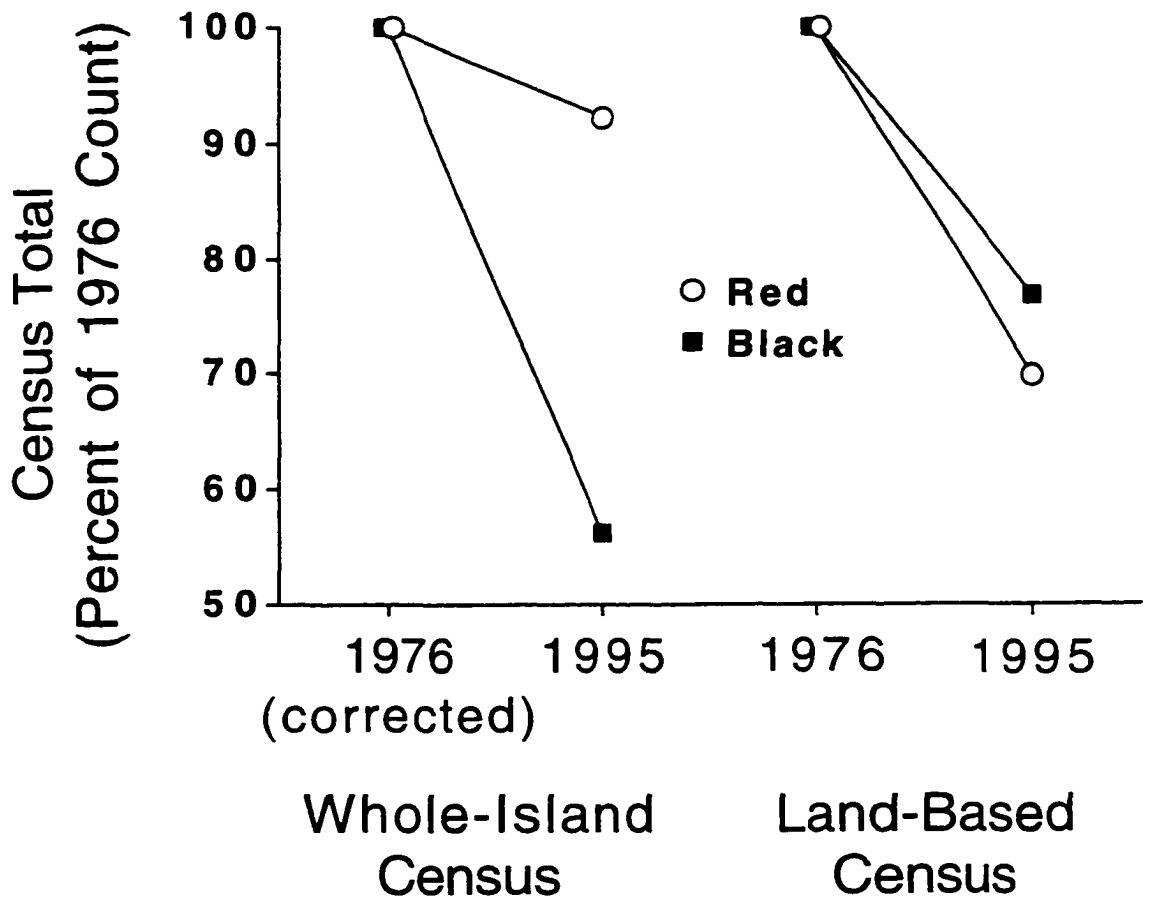


Figure 1.4. Population trends of kittiwakes for whole-island and land-based counts. Count totals Red-legged (Red) and Black-legged (Black) kittiwakes are expressed as percentages of 1976 counts.

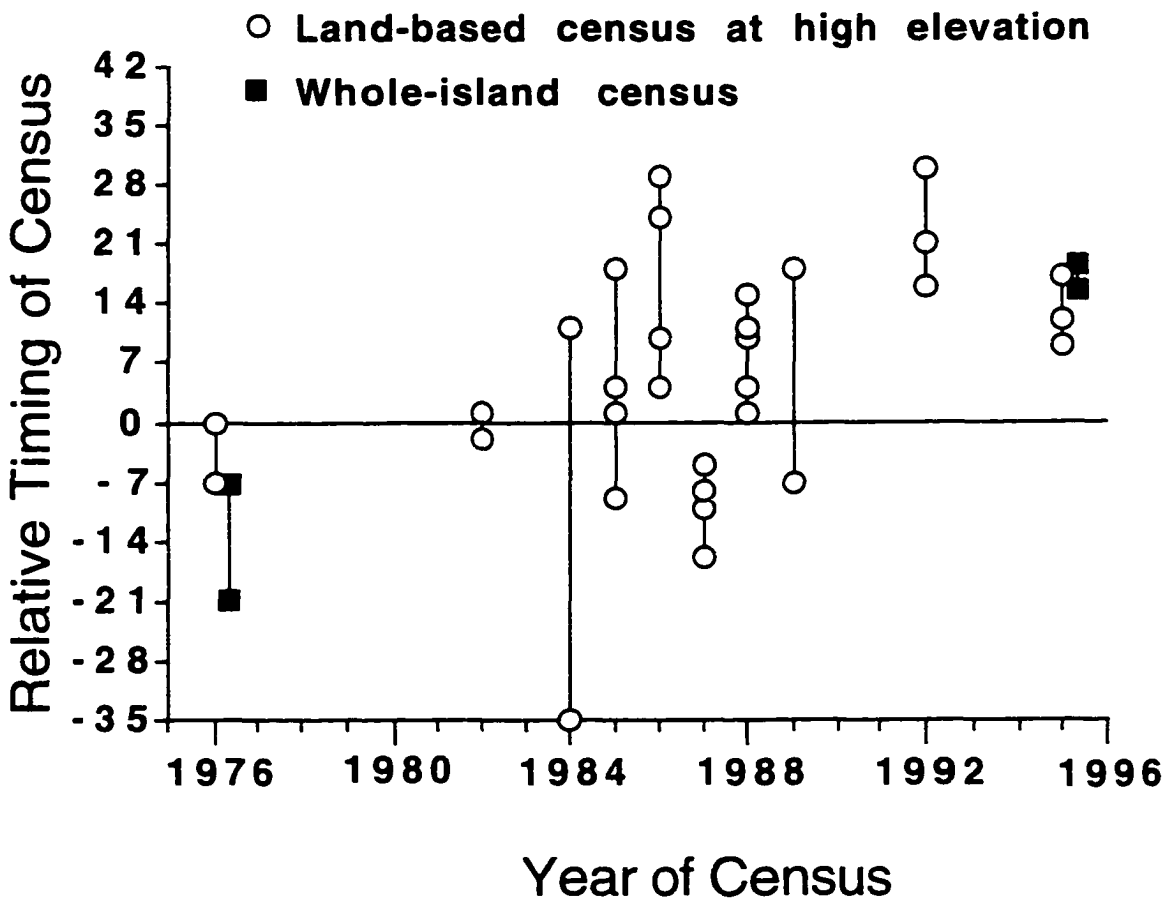


Figure 1.5. Timing of kittiwake censuses on St. George Island. Relative to the breeding chronology of Red-legged Kittiwakes (0 = mean hatch data), land-based counts were conducted approximately 2 weeks later in 1995 than in 1976, and whole-island counts were conducted approximately 4 weeks later in 1995 than in 1976. Points ploted prior to 1984 represent the census interval rather than specific dates. Sources for census dates cited in Figure 1.3 and from unpublished data. Hatch dates for Red-legged Kittiwakes are summarized in Dragoo and Dragoo (1996), Craighead and Oppenheim (1985), and Johnson and Baker (1985). Hatch dates for 1988, 1989 are from Alaska Maritime National Wildlife Refuge (unpublished data).

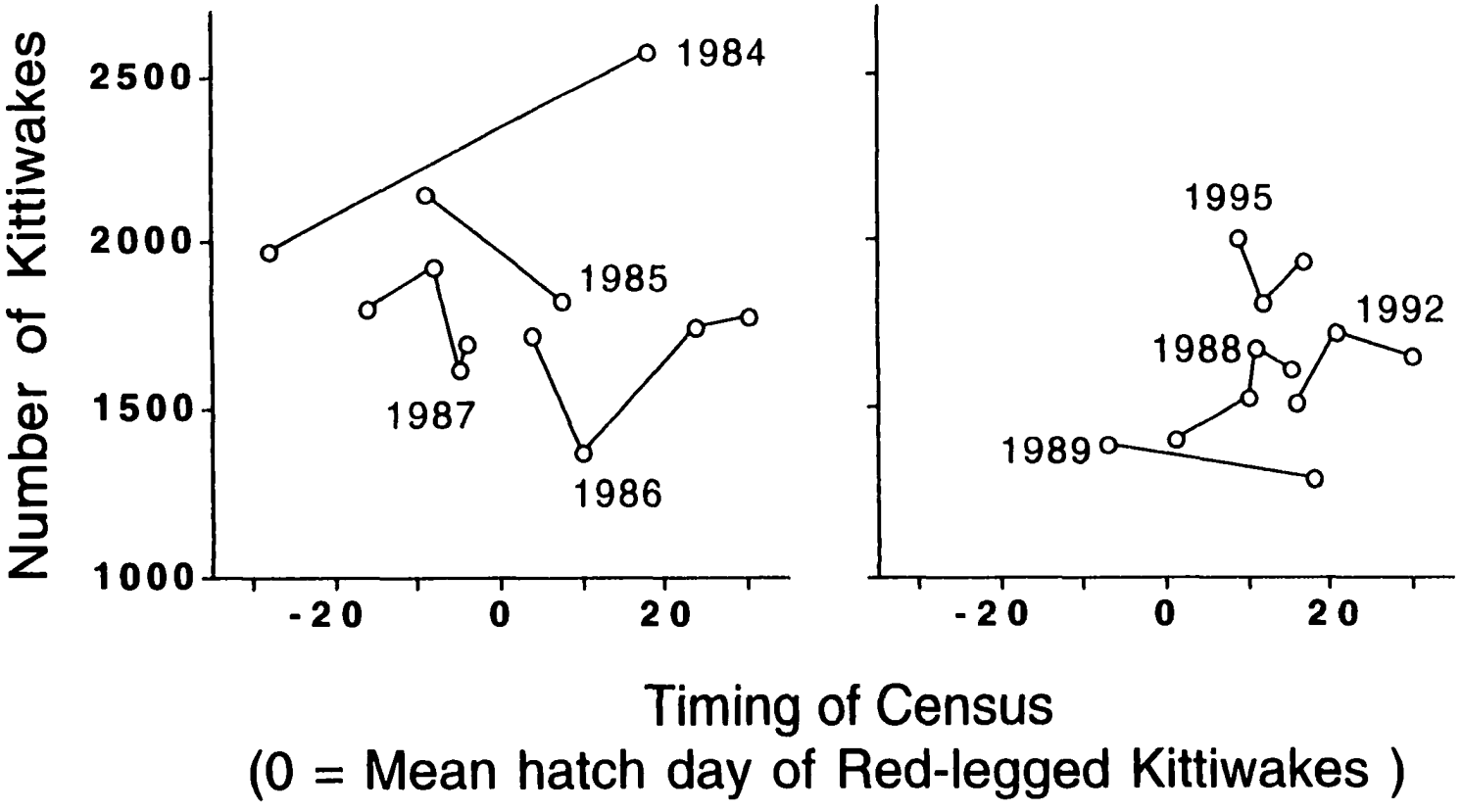


Figure 1.6. Seasonal trends in the attendance of Red-legged Kittiwakes. Data from land-based census plots for years in which counts were replicated. Counts are for "common plots" (see text) at High Bluff and comprise approximately 80% of the land-based census total.

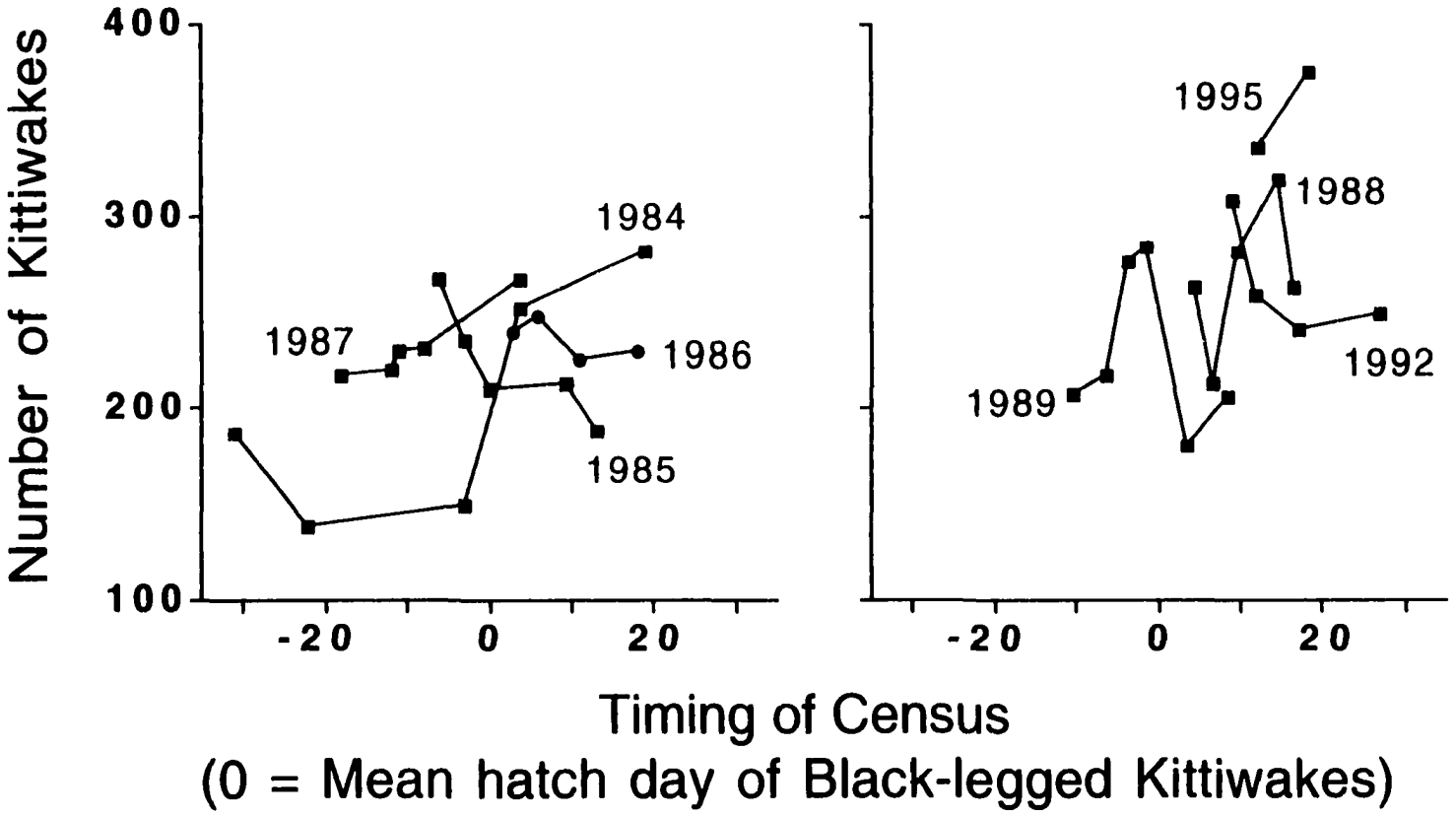


Figure 1.7. Seasonal trends in the attendance of Black-legged Kittiwakes. Data from land-based census plots for years in which counts were replicated. Counts of Black-legged Kittiwakes are for "common plots" (see text) at Tolstoi and comprise approximately 55% of the land-based census total.

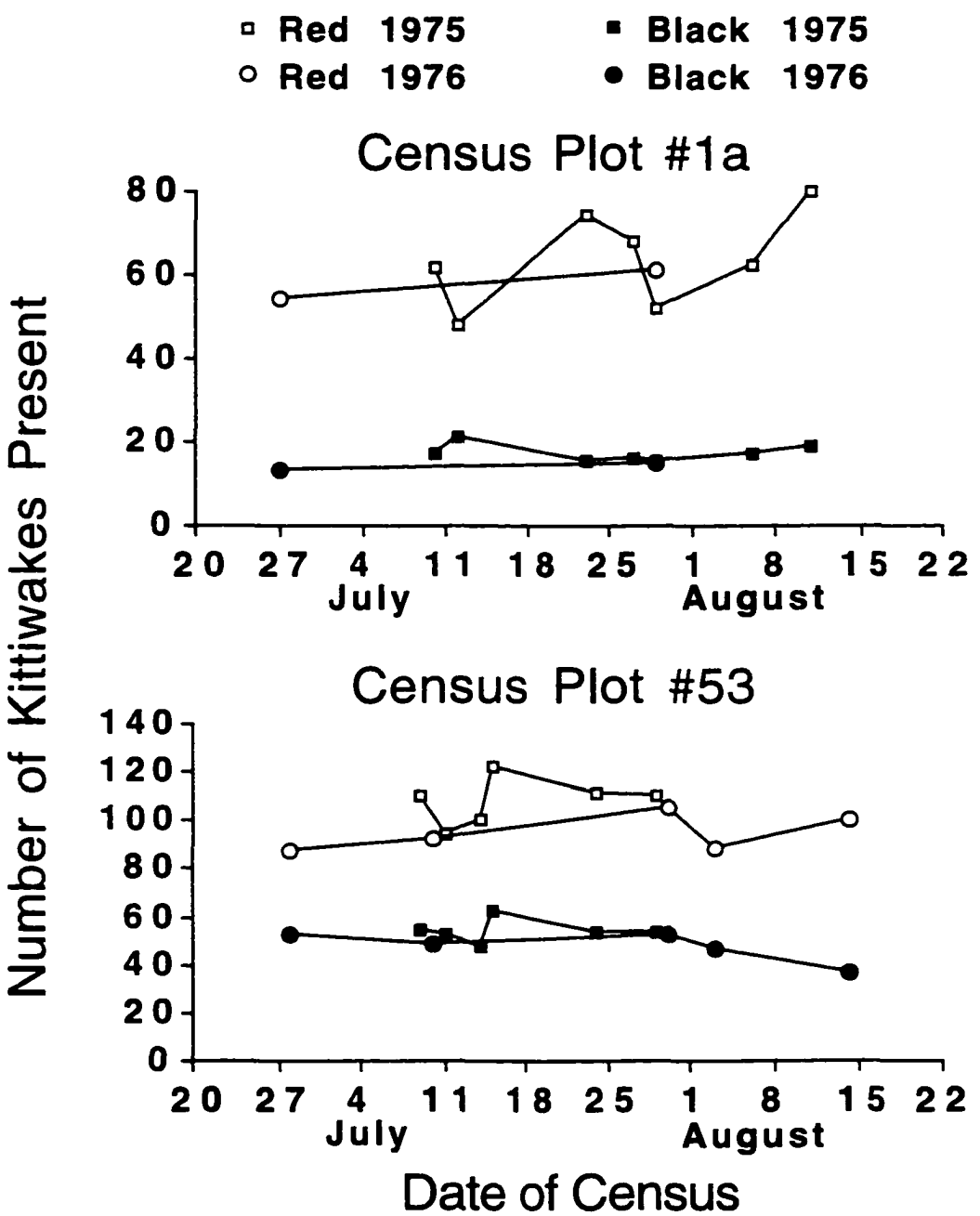


Figure 1.8. Replicated counts of kittiwakes in 1975 and 1976. Counts of Red-legged (Red) and Black-legged (Black) kittiwakes for two land-based census plots (1a and 53) that were replicated in 1975 and 1976. Counts are similar between 1975 and 1976 and there was no apparent seasonal trend in kittiwake numbers within either year.

# COMPETITIVE DISPLACEMENT? AN EXPERIMENTAL ASSESSMENT OF NEST-SITE PREFERENCES OF CLIFF-NESTING GULLS[2]


## ABSTRACT

Red-legged (*Rissa brevirostris*) and Black-legged Kittiwakes (*R. tridactyla*) are colonial seabirds that nest interspersed on cliffs of St. George Island, Alaska, where they potentially compete for nesting ledges. Nesting ledges used by Red-legged Kittiwakes are narrower than those of Black-legged Kittiwakes, are more often located beneath overhangs, and are concentrated on high-elevation cliffs of St. George Island. To determine if the nesting distribution of Red-legged Kittiwakes on St. George Island is shaped by competitive displacement by larger-bodied Black-legged Kittiwakes, I compared realized niches of the two species (determined by measuring physical characteristics of natural nest sites) with fundamental niches of the two species (determined by observing nest-site preferences of kittiwakes on artificial nesting ledges that differed in width, overhang cover, and elevation).

The displacement hypothesis predicted that interspecific overlap in physical characteristics of nest sites would be greater for artificial vs. natural nesting ledges (fundamental niches would overlap to a greater degree than realized niches). In contrast, nest-site preferences of kittiwakes on artificial ledges differed markedly between species and mirrored characteristics of natural nest sites: Red-legged Kittiwakes preferred narrower ledges, Black-legged Kittiwakes preferred wider ledges, and both species preferred ledges located within high density clusters of conspecifics. Thus, I rejected the competitive displacement hypothesis and concluded that interspecific competition does not currently shape the breeding distributions of kittiwakes on St. George Island. Although interspecific competition in the past may have shaped current nest site


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[2] Prepared for submission to *Ecology* as: Kildaw, S. D. Competitive Displacement? An Experimental Assessment of Nest-site Preferences of Cliff-nesting Gulls.

preferences of kittiwakes, the concordance of habitat preferences with interspecific differences in body size, clutch size, and nest size and structure indicate that Red-legged Kittiwakes are uniquely adapted to exploit small ledges.

## INTRODUCTION

Cliff-nesting seabirds commonly breed in mixed-species colonies within which they potentially compete for nest sites. Lack (1968) proposed that where seabirds are not food-limited, nesting habitat would become limiting and promote competition both within and among species for preferred nest sites. Although general availability of nest sites may be rarely limiting to seabirds (Furness and Birkhead 1984, Olsthoorn and Nelson 1990, Wittenburger and Hunt 1985), preferred nest sites within colonies may, nonetheless, be highly contested and limited (Ashmole 1962, Porter and Coulson 1987). Furthermore, both direct observations of competitive displacement (Belopol'skii 1957, Kenyon and Phillips 1965, Maunder and Threlfall 1972, Uspenski 1956) and observations of niche partitioning among species of cliff-nesting seabirds (Lack 1968, Nelson 1970, Squibb and Hunt 1983, Williams 1974) suggest that interspecific competition may control nesting habitat used by seabirds.

Kittiwakes (*Rissa* spp.) are small, fish-eating, gulls that avoid terrestrial and aerial predators by breeding in loose aggregations on sea-side cliffs where they construct nests of mud and vegetation on projecting rock ledges (Cullen 1957). Red-legged (*R. brevirostris*) and Black-legged (*R. tridactyla*) kittiwakes share the basalt cliffs of St. George Island, Alaska, with Thick-billed (*Uria lomvia*) and Common (*U. aalge*) murres, Northern Fulmars (*Fulmarus glacialis*), and Red-faced Cormorants (*Phalacrocorax urile*). Relative to Black-legged Kittiwakes, Red-legged Kittiwakes nest on narrower ledges, use ledges that are more often located beneath overhanging rocks, and nest at extremely high density in high-elevation cliffs of St. George Island (Squibb and Hunt 1983, Hickey and Craighead 1977, Kildaw 1998). Although the two species are ecologically similar, they differ in three fundamental ways: 1) nests of Red-legged

Kittiwakes are smaller that those of Black-legged Kittiwakes (Byrd and Williams 1993) and are more adhesive because they are composed of a greater proportion of mud (Squibb and Hunt 1983); 2) Red-legged Kittiwakes are 15% lighter than Black-legged Kittiwakes (Byrd and Williams 1993) and are the smallest of all cliff-nesting species on St. George Island (Squibb and Hunt 1983); 3) Red-legged Kittiwakes rarely lay more than one egg, while clutches of two eggs are common for Black-legged Kittiwakes on St. George Island (Byrd and Williams 1993).

Although anecdotal observations indicate that both species have co-occurred throughout the range of the Red-legged Kittiwake since the late 1800's and that the distribution of Red-legged Kittiwakes was once more widespread than it is at present (Byrd and Williams 1993), little is known about the evolutionary history of the two species (Byrd and Williams 1993, Baird 1994) or the degree to which interspecific competition affects breeding distributions of kittiwakes on St. George Island. On the other hand, two observations suggest that competitive displacement by Black-legged Kittiwakes may shape nesting habitat used by Red-legged Kittiwakes: 1) characteristics of nest sites used by Red-legged Kittiwakes overlap to a greater degree with those of Black-legged Kittiwakes than with any other cliff-nesting species on St. George Island (Squibb and Hunt 1983); 2) anecdotal observations of aggressive encounters between species suggest that larger-bodied Black-legged Kittiwakes may be dominant over Red-legged Kittiwakes (Byrd and Williams 1993, Kenyon and Phillips 1965).

Understanding the nature of competitive interactions between kittiwake species on St. George Island has conservation implications for the Red-legged Kittiwake, a Bering Sea endemic that breeds at only four known locations (Byrd et al. 1997). The Red-legged Kittiwake is currently a species of concern because approximately 80% its global population breeds on St. George Island (Kildaw 1998), where, for unknown reasons, both kittiwake species experienced a decade of poor reproductive performance during the 1980's, and a 50% decline in population between 1976 and the mid 1980's (Dragoo and Sundseth 1993).

For kittiwakes, acquiring a breeding territory and acquiring food are spatially separate processes; hence, competition among kittiwakes for nesting ledges is purely one for space. In biological systems where space is a contested resource, competitive displacement can be inferred by comparing habitat occupied by a species when its competitors are present, with habitat preferred by a species when its competitors are absent (i.e., its realized vs. its fundamental niche). In other field studies, researchers have used a comparative approach (e.g. Williams 1974) or removal experiments (e.g., Connell 1961) to observe habitat preferences (the fundamental niche) of a species in the absence of its competitors. I was unable to use either of those approaches, and instead, performed a resource-addition experiment to determine habitat preferences of kittiwakes on St. George Island in the absence of competition.

The purpose of this study was to determine whether differences in physical characteristics of nest sites used by the two kittiwake species on St. George Island are a consequence of competitive displacement of Red-legged Kittiwakes to marginal nesting habitat by larger-bodied Black-legged Kittiwakes. I determined the realized niche of Red-legged and Black-legged Kittiwakes by measuring physical characteristics of natural kittiwake nest sites on St. George Island and determined habitat preferences of both species by observing their use of artificial nesting ledges that differed in width, overhang cover, and elevation. Kittiwakes colonized newly-established artificial ledges in the absence of competition because numerous unoccupied ledges were available to any individual that may have been displaced from a contested ledge. The competitive displacement hypothesis predicts that interspecific overlap in physical characteristics of nest sites will be greater for artificial vs. natural nest sites, and implies that Red-legged Kittiwakes are displaced to inferior nesting habitat and thus, when given a choice, should not prefer narrow, overhung, high-elevation ledges that they are observed to use in nature.

Previous research suggests that seabirds are attracted to high-density aggregations of conspecifics (Porter and Coulson 1987, Ashmole 1962, Duffy 1983). To investigate effects of social environment on habitat preferences of kittiwakes, I distributed artificial

ledges among areas that differed in both density and species composition of natural nest sites and predicted that kittiwakes would prefer artificial ledges located in areas where conspecifics nest at high densities.

## MATERIALS AND METHODS

### *Study Area*

Field work was conducted from May-August in 1994 and 1995 on St. George Island, Alaska, the southernmost of the Pribilof Islands (56° 35' N 169° 35' W). St. George Island is located in the southeastern Bering Sea and is the site of one of the largest seabird colonies in the North Pacific, including estimated breeding populations of 194,000 Red-legged and 62,500 Black-legged Kittiwakes (Kildaw 1998).

### *Ledge Measurements*

I accessed 225 Red-legged Kittiwake nest sites and 203 Black-legged Kittiwake nest sites using a climbing rope or ladder at 20 sampling plots on St. George Island that were not randomly selected (due to logistic constraints), but were located in representative kittiwake nesting habitat at both low and high elevation. I used methods modified from Squibb and Hunt (1983) to measure the following characteristics of each nest site:

*Ledge Width* (cm) = horizontal distance from base of back wall to precipice as measured through the nest center (Fig. 2.1a). Initially measured along slope of ledge in the field and later trigonometrically transformed to a horizontal distance using Ledge Slope.

*Ledge Length* (cm) = maximum, horizontal distance between points where ledge merges with backwall on either side of the nest site (Fig. 2.1a).

*Ledge Slope* (°) = angle formed between ledge surface and horizontal plane such that a ledge tilted seaward has a slope < 0° (Ledge Slope of Fig. 2.1b = -13°).

*Backwall Slope* (°) = angle formed between backwall surface and horizontal plane such that an overhanging backwall has a slope < 90° (Backwall Slope of Fig. 2.1b = 47°).

*Enclosure* = degree of sidewall protection of the nest site. Measured at nest level by horizontally spanning rock walls on either side of the nest with a 50 cm cord (centered over nest) and determining where the cord bisected the nest (Enclosure of Fig. 2.1a = 2): 1 = < half of nest is enclosed; 2 = center of nest is enclosed; 3 = entire nest is enclosed.
*Backwall Height* (cm) = vertical distance from a point directly beneath the nest center to the backwall (Fig. 2.1b; no measurement possible if Backwall Slope ≥ 90°).
*Overhang Presence* = presence (1) or absence (0) of a rock overhang < 50 cm above a point on the ledge directly beneath the nest center (calculated from Backwall Height measurement).
*Standard Overhang* - presence (1) or absence (0) of a rock overhang < 50 cm above a point on the ledge 10 cm from base of backwall (calculated from standardized Backwall Height measurement).

I measured Ledge Width and Ledge Length with a cord marked in 5 cm increments and measured Backwall Height with a 200-cm cord attached to a lead plumb. I measured Ledge Slope and Backwall Slope using a homemade clinometer constructed from wooden calipers, a line level, and a protractor. To facilitate comparisons between my data and those of Squibb and Hunt (1983), I generated the binary variable Overhang Presence by collapsing the continuous variable Backwall Height into two categories: < 50 cm, and ≥ 50 cm. Backwall Height and Overhang Presence are not directly comparable between species because Backwall Height was measured at the center of the nest and nest size differs between species: mean external radius of a Black-legged Kittiwake nest is 12 cm, but that of a Red-legged Kittiwake nest is only 9 cm (Byrd and Williams 1993). Using simple trigonometry, I adjusted Backwall Height measurements to a standard distance of 10 cm from the base of the backwall by assuming that surfaces of both the ledge and backwall were uniform and that Backwall Height was initially measured at either 9 cm or 12 cm from the base of the backwall (for nests of Red-legged and Black-legged Kittiwakes, respectively). I then used standardized Backwall Height measurements to generate the binary variable Standard Overhang. I do not include

Backwall Height in further analyses because it was measured only to generate Overhang Presence and Standard Overhang variables.

All measurements were somewhat imprecise because of the irregular nature of ledge surfaces. Furthermore, Width and Ledge Slope measurements were complicated by presence of nesting material on the ledge. Ledge measurements departed from those performed by Squibb and Hunt (1983) in two ways: 1) I measured Width along the slope of the ledge and trigonometrically converted it to a horizontal measurement because direct estimates of horizontal width were extremely subjective, and 2) I determined Overhang Presence from Backwall Height measurements made at the surface of the ledge, not the surface of the nest, because I measured many ledges at a stage in the breeding season when nests were not fully developed.

I compared means of seven ledge measurements between species using the normal approximation of Mann-Whitney $U$ tests for variables that were continuously distributed and log-likelihood ratio ($G$) tests for variables that were ordinal. I set $\propto = 0.05/7 = 0.0071$ for each comparison to limit experiment-wise $\propto$ to no more than 0.05 in these tests. In addition, I performed a discriminant analysis on ledge variables to determine degree of multivariate separation of ledges used by Red-legged and Black-legged Kittiwakes.

*Artificial Ledges*

I constructed wide artificial ledges from rough-cut "1 x 8" boards that were 20 cm wide x 2.5 cm thick x 30 cm long, and narrow artificial ledges from planed "2 x 4" boards that were 9 cm wide x 4.4 cm thick x 30 cm long. I nailed narrow and wide ledges to opposite ends of backing plates that were 20 cm wide x 2.5 cm thick x 40 cm tall, to create structures with two ledge surfaces and then painted these surfaces with a mortar-sand slurry to facilitate the adhesion of nest material to ledges. I attached each ledge structure to the cliff by rappelling down a climbing rope and using a Hilti DX350 charge-driven gun to shoot 7.3 cm - long concrete nails through the backing plate into the rock

behind it. I attached ledge structures side-by-side in complementary pairs ("clusters" hereafter): one structure with the narrow ledge oriented upper-most and the other with the wide ledge oriented upper-most. Thus, four artificial ledges were available within each ledge cluster: narrow-upper and wide-upper ledges that lacked artificial overhangs, and narrow-lower and wide-lower ledges that were located beneath upper ledges which provided partial (45%) and complete (100%) overhang coverage, respectively. I attached between 1 and 5 clusters of artificial ledges at 17 high-elevation locations and 28 low-elevation locations (ledge plots) and attached totals of 34 ledge clusters in 1994 and 88 ledge clusters in 1995. Boundaries of artificial ledge plots were defined by the boundaries of nest aggregations within which ledge clusters were established. In both years artificial ledges were attached approximately 2 - 4 weeks before egg laying was initiated by kittiwakes.

I determined the relative abundance (species composition) of natural nests of Red-legged and Black-legged Kittiwakes for each artificial ledge plot in late June (late incubation) of the year the plot was established. Ledge plots where the proportion of natural nests of Red-legged or Black-legged Kittiwakes was > 80% were considered "red-legged"or "black-legged" in species composition, respectively. Plots where the proportion of either species did not exceed 80% were considered "mixed" in species composition. Although I did not directly measure density of natural nest sites in the vicinity of artificial ledges, I subjectively assigned a density category (low or high) to each artificial ledge plot based on proximity of artificial ledges and natural nest sites. I classified a ledge plot as high density if it contained at least 10 natural nests and most artificial ledges were intermixed with natural nests. In addition, I classified plots that included > 20 natural kittiwake nests as high density even if artificial ledges on that plot were located peripherally to natural nest sites. All other artificial ledge plots were classified as low density sites. Although my density classification procedure was subjective, it accounted for marked differences among plots in density of natural nests in the immediate vicinity (< 5 m) of artificial ledges.

Nest density and species composition have the potential to confound the relationship between ledge use and elevation because both differ markedly between low-elevation, and high-elevation areas on St. George Island. Only with an adequately-replicated, three-factor experimental design would it have been possible to separate effects of elevation, nest density, and species composition on patterns of ledge use by kittiwakes. An experiment such as this, though theoretically appealing, could not be implemented in the field because all combinations of the three factors do not exist on St. George Island: few Black-legged Kittiwakes nest within high-elevation areas and few Red-legged Kittiwake areas were accessible at lower elevations. Therefore, I systematically distributed artificial ledges among plots that differed in elevation, density, and species composition in as balanced a manner as possible. Although I lacked the appropriate data for a three-factor analysis, I performed two-factor tests and controlled for effects of the third factor by restricting each analysis within a single level of the third factor.

Weather permitting, I monitored artificial ledges every 3 - 5 days between May - August in both 1994 and 1995. On each visit, I recorded developmental status of each ledge and number and species of birds present. Ledge status was categorized as one of the following: 1) Wood = no evidence of nest building; 2) Mud Roost = ranging from a small clump, to a larger unshaped mass of nest material; 3) Nest Platform = a disk of nest material that was a minimum of 15 - 20 cm in diameter and at least 5 cm thick; 4) Cup Nest = an advanced nest structure with a depression capable of holding eggs. I summarized observations for each artificial ledge by identifying the maximum stage of nest development and determining which species occupied the ledge at that time. In all analyses I only used data from ledges that attained Nest Platform status during the first summer that they were available to kittiwakes because Mud Roosts were ephemeral and only intermittently attended by kittiwakes. I also omitted data from three ledge structures that fell from the cliff during the breeding season in 1995.

Interspecific competition did not influence initial occupation of artificial ledges

because at all times kittiwakes were free to choose among ledges that differed in characteristics of width, overhang cover, elevation, density, and species composition. Throughout this paper I assume that differential use of artificial ledges by kittiwakes indicated a preference for the physical and/or social characteristics of ledges that were selected; however, sites preferred by kittiwakes within the context of this study may not be "ideal" nest sites for a given species because other factors not considered in my analysis may also shape ledge use by kittiwakes.

I used *G* tests to compare, both within and between species, use of ledges differing in width and overhang cover. For these analyses, I used data from only the first ledge of each cluster of four that attained a "nest platform" status because ledge options available to later-arriving kittiwakes were thereafter restricted. I also used *G* tests to compare width and overhang cover of natural and artificial ledges that were used by each kittiwake species. For ledge-width analyses, I generated expected frequencies by determining the proportion of natural ledges with width measurements falling above and below 17.7 cm, the midpoint between average widths of narrow (12.3 cm) and wide (23.3 cm) artificial ledges (Fig. 2.2). Expected frequencies for overhang cover were determined directly from Standard Overhang values.

For analyses that evaluated effects of elevation, density, and species composition on use of artificial ledges by kittiwakes, I considered the plot, rather than the ledge cluster, as the experimental unit. Thus, I used data from every ledge that attained "nest platform" status; however, I excluded data from ledges that were occupied under circumstances where kittiwakes were not free to choose between narrow and wide ledges within that plot (i.e., ledges occupied after all narrow or wide ledges within a plot had been occupied by kittiwakes). For each plot I determined the proportion of artificial ledges used by each species of kittiwake and compared ledge use between low-elevation plots and high-elevation plots with a Mann-Whitney *U* test. I further evaluated interactive effects of elevation, density, and species composition on ledge use by performing ANOVAs on rank-transformed data (because raw data did not meet

distribution assumptions of parametric tests). In a two-factor ANOVA that evaluated effects of density and species composition on ledge use by kittiwakes, I controlled for elevation by restricting the analysis to low-elevation plots only. For this analysis, I excluded data from 5 low-elevation plots that were established on barren cliff faces and hence could not be assigned a species composition category. In addition, I evaluated effects of density and elevation on ledge use by performing a two-factor ANOVA that controlled for species composition by restricting the analysis to "red-legged" plots only.

Unless otherwise specified, all statistical tests were performed using SAS 6.11 for Windows with $\alpha$ set at 0.05, on data pooled from both years of the study.

## RESULTS

### *Natural Ledges*

Interspecific differences in characteristics of natural ledges corresponded well with those reported by Squibb and Hunt (1983). Relative to Black-legged Kittiwakes, Red-legged Kittiwakes nested on ledges that were significantly narrower (Fig. 2.2), shorter, more enclosed, and had greater overhang cover (Table 2.1). In contrast, Ledge Slope and Backwall Slope did not differ between species (Table 2.1). Although both measures of overhang cover were significantly greater for nest sites of Red-legged Kittiwakes, the magnitude of the difference was less for Standard Overhang (0.13) than for Overhang Presence (0.25; Table 2.1). I used Standard Overhang measurements in all subsequent analyses of overhang cover because, unlike Overhang Presence, it was not biased by interspecific differences in nest size.

Despite significant interspecific differences in mean measurements of natural ledges, there was still substantial overlap in frequency distributions of ledge measurements between species (e.g., Ledge Width: Fig. 2.2; Table 2.1). Furthermore, discriminant analysis of ledge measurements indicated that there was considerable multivariate overlap in physical characteristics of natural ledges used by Red-legged and Black-legged Kittiwakes. A cross-validation analysis of a discriminant model that

incorporated six variables (Ledge Width, Ledge Length, Ledge Slope, Backwall Slope, and Backwall Height) correctly classified 76% of Red-legged Kittiwake nesting ledges and 70% of Black-legged Kittiwake nesting ledges.

*Artificial Ledges*

Relative use of narrow vs. wide artificial ledges differed between species ($G_{1\,df}$ = 43, $P < 0.001$) and departed from unity (the null expectation) within each species: 94% of ledges used by Red-legged Kittiwakes were narrow ($G_{1\,df} = 31$, $P < 0.001$), whereas 80% of ledges used by Black-legged Kittiwakes were wide ($G_{1\,df} = 14$, $P < 0.001$) (Fig. 2.3). Relative to natural nesting ledges, Red-legged Kittiwakes used a greater proportion of narrow artificial ledges ($G_{1\,df} = 9.6$, $P < 0.001$) and Black-legged Kittiwakes used a greater proportion of wide artificial ledges ($G_{1\,df} = 6.1$, $P < 0.001$). Thus, interspecific overlap in ledge width was greater for natural than for artificial ledges.

Relative use of artificial ledges with and without artificial overhangs did not differ between Red-legged and Black-legged Kittiwakes ($G_{1\,df} = 0.01$, $P = 0.9$). Both species preferred upper ledges that lacked artificial overhangs: 70% of ledges used by Red-legged Kittiwakes ($G_{1\,df} = 5.3$, $P = 0.02$) and 69% of ledges used by Black-legged Kittiwakes ($G_{1\,df} = 5.0$, $P = 0.03$) lacked artificial overhangs (Fig. 2.4). Although all upper artificial ledges lacked artificial overhangs, I measured a sample of 50 upper ledges and found that 15% were, by chance, located beneath natural overhangs. Therefore, I made an assumption that 15 % of upper artificial ledges used by kittiwakes also had natural overhangs and found that overhang cover did not differ between natural and artificial ledges for either Black-legged ($G_{1\,df} = 0.90$, $P > 0.05$) or Red-legged Kittiwakes ($G_{1\,df} = 0.88$, $P > 0.05$). Thus, interspecific overlap in overhang cover was no greater for natural than for artificial ledges.

Use of artificial ledges by both species differed significantly between high-elevation plots and plots at lower elevations. Ledge use by Red-legged Kittiwakes was significantly greater (Mann-Whitney $U$, $z = 2.37$, $P = 0.02$) at high elevation (Fig. 2.5). In

contrast, ledge use by Black-legged Kittiwakes was greater (Mann-Whitney $U$, $z = 3.00$, $P = 0.003$) at low elevation (Fig. 2.5). These analyses suggest that elevation influenced ledge use by kittiwakes but do not take into account marked differences in the density and species composition of natural nest sites that exist between high and low elevation plots. At high elevation, 15 of 17 artificial ledge plots were "red-legged" in species composition and, of these, most (9 of 15) were high-density plots. In contrast, at low elevation, only 5 of 28 plots were "red-legged" in species composition and, of these, only 2 were high-density plots.

To evaluate effects of nest density and species composition on use of artificial ledges by kittiwakes, I performed two-factor ANOVAs that controlled for elevation by restricting the analysis to low-elevation plots only. Use of artificial ledges by Red-legged Kittiwakes was greatest on plots established in areas where natural nests of Red-legged Kittiwakes occurred at high density (density, $F_{1,17\,df} = 4.6$, $P = 0.05$; species, $F_{2,17\,df} = 3.9$, $P = 0.04$; Fig. 2.6). There was no density x species composition interaction ($F_{2,17\,df} = 1.3$, $P = 0.3$). Use of artificial ledges by Black-legged Kittiwakes was greatest in areas where Black-legged Kittiwakes nested at high density (density, $F_{1,17\,df} = 8.7$, $P = 0.009$; species, $F_{2,17\,df} = 6.9$, $P = 0.006$)(Fig. 2.7). A significant density x species composition interaction ($F_{2,17\,df} = 4.2$, $P = 0.03$) indicted that the relationship between nest density and ledge use by Black-legged Kittiwakes differed among species composition classes: it was positive for "black-legged" plots and mixed-species plots, but was negative for "red-legged" plots.

To evaluate effects of nest density and elevation on use of artificial ledges by Red-legged Kittiwakes, I performed a two-factor ANOVA that controlled for species composition by restricting the analysis to "red-legged" plots only. Use of artificial ledges by Red-legged Kittiwakes was greater on high-density plots ($F_{1,21\,df} = 66$, $P = 0.0001$), but did not differ between high-elevation and low-elevation plots ($F_{1,21\,df} = 0.08$, $P = 0.77$; Fig. 2.8). In addition, the density x elevation interaction was not significant ($F_{1,21\,df} = 0.26$, $P = 0.61$). Thus, my results suggest effects of density, but not elevation on ledge use by Red-legged Kittiwakes.

These results indicate that nest site selection by kittiwakes is affected by both physical (ledge width and overhang cover) and social (nest density and species composition) characteristics of nest sites. I evaluated the relative importance of physical and social characteristics of nest sites to prospecting kittiwakes by comparing percent use of artificial ledges with preferred and non-preferred physical characteristics between ledge plots with preferred and non-preferred social environments. In this analysis, I classified the social environment of an artificial ledge as "preferred" if it was located within same-species or mixed species ledge-plots where kittiwakes nested at high density. I classified the physical characteristics of a ledge as "preferred" if, for Red-legged Kittiwakes, the ledge was narrow and lacked an artificial overhang and, for Black-legged Kittiwakes, the ledge was wide and lacked an artificial overhang. I found that for both species, social factors had greater influence on ledge use than did physical characteristics (Fig. 2.9): in preferred social environments, ledges with non-preferred physical characteristics were used at a significantly greater rate than were ledges with preferred physical characteristics that were located in non-preferred social environments (Red-legged Kittiwakes, Mann-Whitney $U$, $z = 2.4$, $P < 0.01$: Black-legged Kittiwakes, Mann-Whitney $U$, $z = 2.1$, $P < 0.03$).

## DISCUSSION

The competitive displacement hypothesis predicted that both kittiwake species would display a preference for wide ledges located at low elevations and that overlap of ledge characteristics of the two species would be greater for artificial vs. natural nest sites. My results contradicted these predictions: when given a choice between narrow and wide artificial ledges, Red-legged Kittiwakes preferred narrow ledges, Black-legged Kittiwakes preferred wide ledges, and overlap of ledge width between species was less for artificial than for natural nest sites. Thus, I conclude that Red-legged Kittiwakes are not competitively displaced to narrow ledges by Black-legged Kittiwakes; rather, they actively select the narrow ledges that they occupy in nature.

My measurements of the Overhang Presence of natural kittiwake nest sites (Table 2.1) were comparable to those of Squibb and Hunt (1983) and indicated a large difference in the overhang cover of nests of Red-legged and Black-legged Kittiwakes. However, Overhang Presence was measured at the center of the nest and, hence, was biased by interspecific differences in nest size. When I removed this bias and generated the variable Standard Overhang, the difference in overhang cover between kittiwake species was halved (Table 2.1). Data from artificial ledges indicated that both species avoided lower ledges with artificial overhangs (Fig. 2.4) and that overhang cover was no greater for artificial than for natural nesting ledges. Although these observations suggest that Red-legged Kittiwakes are not competitively displaced to ledges located beneath overhangs by Black-legged Kittiwakes, my results are inconclusive because the design of artificial ledge structures inextricably confounded the presence or absence of an overhang with four other characteristics of artificial ledges: (1) only lower ledges were equipped with artificial overhangs (and lower ledges may be avoided by kittiwakes for other reasons); (2) ledges with artificial overhangs were approximately 3.3 cm narrower than ledges that lacked overhangs (20.3 cm vs. 23.3 cm for wide ledges and 8.9 cm vs 12.1 cm for narrow ledges); (3) all ledges with artificial overhangs had wooden back walls while all upper ledges that lacked overhangs had natural rock back walls; and (4) 15 % of upper ledges were, by chance, located beneath rock overhangs. Thus, the apparent preference of kittiwakes for artificial ledges lacking overhangs may have arisen through the influence of these other factors and not overhang cover itself. Alternately, overhang cover may be unimportant to Red-legged Kittiwakes. If, on average, narrow ledges have greater overhang cover than wide ledges (for geological reasons), then greater overhang cover of natural ledges used by Red-legged Kittiwakes could simply be a secondary consequence of their preference for narrow ledges. Unfortunately I could not test this hypothesis because I did not measure physical characteristics of natural ledges available to kittiwakes.

Initial analyses of elevational trends in use of artificial ledges by kittiwakes

suggested that Red-legged Kittiwakes preferred artificial ledges located in high-elevation areas and that Black-legged Kittiwakes preferred artificial ledges located in low-elevation areas (Fig. 2.5). However, further analyses indicated that both species preferred artificial ledges located within plots where conspecifics nested at high density (Figs. 7 and 8) and revealed that elevational analyses were confounded by marked differences in density and species composition between high-elevation and low-elevation areas of St. George Island. Specifically, results of an elevation x density ANOVA indicated that elevation *per se* did not influence ledge use by Red-legged Kittiwakes; rather, they suggest that Red-legged Kittiwakes were attracted to artificial ledges at high elevations because conspecifics nested there at high density (Fig. 2.8). Moreover, observed differences in the elevational stratification of kittiwakes between St. George Island and Bering Island (one of the Russian Commander Islands off the coast of Kamchatka) also suggest that elevation does not influence nest-site selection by kittiwakes: on Bering Island, Red-legged Kittiwakes are more abundant at lower rather than higher elevations (A. Kondratyev, pers. comm.).

Although my results can explain the perpetuation of elevational patterns in the distribution of kittiwakes on St. George Island (high-elevation areas are disproportionately attractive to prospecting Red-legged Kittiwakes), I can only speculate about how these patterns developed in the first place. I hypothesize that differences in the elevational distribution of Red-legged and Black-legged Kittiwakes may have arisen through an interaction between nest-site preferences of kittiwakes and differences in the availability of nesting substrate between low-, and high-elevation areas. I did not measure availability of potential nesting ledges for kittiwakes; however, ledges appear to be narrower and more densely packed at high elevation because volcanic rock composing high-elevation cliffs is more finely fractured and less columnar than rock at low elevation (pers. obs.). Therefore, at high elevation, density-biased recruitment could, through positive feedback, enhance the density of Red-legged Kittiwakes to a greater degree than was possible at low elevation. Hence, the current distribution of Red-legged Kittiwakes on St. George Island may represent an stable state that was an inevitable product of the

distribution of potential breeding sites and density biased recruitment.

Forbes and Kaiser (1994) explain the attraction of cliff-nesting seabirds to established breeding areas by suggesting that prospectors must overcome an "information barrier" to colonize unoccupied nesting habitat: they must weigh fitness costs of intense interspecific competition for limited nest sites that occur within established breeding areas against unknown risks associated with pioneering unoccupied nesting habitat. In addition, prospecting individuals potentially obtain information about habitat quality from not only the presence, but also the reproductive success, of conspecifics (Boulinier et al. 1996). Prospecting kittiwakes may be attracted to high density groups because anti-predatory, "selfish herd" advantages, which operate within any group of organisms, increase as a positive function of group size (Bertram 1978) and potentially enhance reproductive success. Although predation is not currently a significant source of nest failure on St. George Island (pers. obs.), kittiwake nest site preferences may have been shaped by past predation and may persist as a "ghost of predation past" in the absence of active reinforcement.

I found that social, rather than physical, factors had a greater influence on the suitability of nest sites to kittiwakes (Fig. 2.9). Although nest sites are not generally limiting on St. George Island (Byrd and Williams 1993), the attraction of kittiwakes to preferred social environments was so great that, in high-density plots, artificial ledges with preferred physical characteristics became limiting within two weeks of being established, and, thereafter, individuals occupied ledges with less-preferred physical characteristics (pers. obs.). Other researchers have also observed that cliff-nesting seabirds compete intensely for nest sites and may use physically sub-optimal sites within established breeding areas. Black-legged Kittiwakes nesting on window ledges of an abandoned warehouse in northern England competed intensely for a limited number of nest sites located at the center of the colony (Porter and Coulson 1987). When additional nesting ledges were provided, kittiwakes occupied more than 80% of those located within the preferred center of the colony but did not use physically identical ledges located at the

colony periphery (Porter and Coulson 1987). Ashmole (1962) reported that Black Noddies (*Anous tenuirostis*) on Ascension Island competed intensely for nest sites located within existing breeding colonies even though suitable, unoccupied nesting habitat was available on nearby cliffs. Nest sites were so limited within existing noddy colonies that some individuals attempted to breed on ledges that were too narrow to effectively hold eggs (Ashmole 1962). Similarly, Duffy (1983) reported that intraspecific competition within two species of ground-nesting "guano birds", the Guanay Cormorant (*Phalacrocorax bougainvillii*) and the Peruvian Booby (*Sula variegata*), displaced later-arriving breeders to less-preferred habitat at the periphery of monospecific breeding aggregations. Lastly, intense intraspecific competition and nest site limitiation within socially preferred areas may explain why seabirds nesting in Aberdeenshire, Scotland used physically atypical nest sites even though suitable nest sites were available nearby (Olsthoorn and Nelson 1990), and may further explain paradoxical observations of an absence of overt interspecific competition for nest sites despite great overlap in physical characteristics of nest sites used by different species of seabirds (Olsthoorn and Nelson 1990, Squibb and Hunt 1983).

In summary, results of artificial ledge experiments indicated that Red-legged Kittiwakes preferred narrow artificial ledges, Black-legged Kittiwakes preferred wide ledges, both species preferred ledges located in areas where conspecifics nest at high densities, and ledge use was influenced to a greater degree by social vs. physical characteristics of nest sites. Where use patterns of artificial ledges departed from use patterns of natural ledges, the difference was in the direction of reduced overlap between species on artificial ledges, suggesting that realized niches of both kittiwake species on St. George Island are not restricted by interspecific competition relative to the fundamental niches of both species. Thus, I conclude that Red-legged Kittiwakes are not competitively displaced by Black-legged Kittiwakes; rather, they prefer the narrow, high elevation ledges that they use in nature. This conclusion is further supported by comparable inter-specific overlap in the physical characteristics of ledges between 1976

and the mid 1990's (Table 2.1) despite a 50% reduction in populations (and, presumably, interspecific competition for nest sites) of both species on St. George Island over this same time period ( Dragoo and Sundseth 1993). In contrast, the competitive displacement hypothesis predicted greater interspecific overlap of realized niches during conditions of relaxed interspecific competition.

In discarding the competitive displacement hypothesis, I do not rule out the possibility that current distributions and nest site preferences of kittiwakes may have been shaped by interspecific competition during the evolutionary history of the two species and, hence, may be a "ghost of competition past". Alternately, differing nest site preferences of the two kittiwake species might reflect ecological specialization that is unrelated to interspecific competition. Narrow ledges are potentially a valuable resource to cliff-nesting seabirds because they are less accessible to both terrestrial and aerial predators. Red-legged Kittiwakes are smaller bodied, build smaller more adhesive nests, and lay fewer eggs than Black-legged Kittiwakes (Byrd and Williams 1993, Squibb and Hunt 1983) and, thus, may be uniquely adapted to exploit the narrow ledges they use in nature. Regardless of which selective forces have shaped nest site preferences of kittiwakes, physical and behavioral adaptations of the Red-legged Kittiwake for narrow ledges suggests that nest site preferences of the two species diverged in the distant evolutionary past.

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## LITERATURE CITED

Ashmole, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General biology. Ibis 103b:235-273.

Baird, P. H. 1994. Black-legged Kittiwake (*Rissa tridactyla*). Pages 1-26 *in* A. Poole and F. Gill, editors. The birds of North America, no. 92. Academy of Natural Sciences of Philadelphia and American Ornithologists' Union, Philadelphia, Pennsylvania, USA.

Belopol'skii, L. O. 1957. Ecology of sea colony birds of the Barents sea. Israel program for scientific translations (1961), Jerusalem, Israel.

Bertram, B. R. C. 1978. Living in groups: predators and prey. Pages 64-96 *in* J. R. Krebs and N. B. Davies, editors. Behavioural ecology: an evolutionary approach. Blackwell, Oxford, England.

Boulinier, T., E. Danchin, J. Monnat, C. Doutrelant, and B. Cadiou. 1996. Timing of prospecting and the value of information in a colonial breeding bird. Journal of Avian Biology. 27:252-256.

Byrd, G. V., and J. C. Williams. 1993. Red-legged Kittiwake (*Rissa brevirostris*). Pages 1-11 *in* A. Poole and F. Gill, editors. The birds of North America, no. 60. Academy of Natural Sciences of Philadelphia and American Ornithologists' Union, Philadelphia, Pennsylvania, USA.

Byrd, G. V., J. C. Williams, Y. B. Artukhin, and P. S. Vyatkin. 1997. Trends in populations of Red-legged Kittiwake (*Rissa brevirostris*), a Bering Sea endemic.

Bird Conservation International. 7:167-180.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42: 710-23.

Cullen, E. 1957. Adaptations in the kittiwake to cliff-nesting. Ibis 99:275-302.

Dragoo, B. K., and K. Sundseth. 1993. The status of northern fulmars, kittiwakes, and murres at St. George Island, Alaska, in 1992. Unpublished report. U. S. Fish and Wildlife Service, Homer, Alaska, USA.

Duffy, D.C.1983. Competition for nesting space among Peruvian guano birds. Auk 100:680-688.

Forbes, L. S., and G. W. Kaiser. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. Oikos 70:377-384.

Furness, R. W., and T. R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655-656.

Hickey, J. J., and F. L. Craighead. 1977. A census of seabirds on the Pribilof Islands. U. S. Department of Commerce, NOAA, OCSEAP, Final Report 2:96-195.

Kenyon, K. W., and R. E. Phillips. 1965. Birds from the Pribilof Islands and vicinity. Auk 82:624-635.

Kildaw, S. D. 1998. Population status and patterns of distribution and productivity of kittiwakes on St. George Island, Alaska. Ph. D. thesis. University of Alaska Fairbanks. Fairbanks Alaska, USA.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.

Maunder, J. E., and W. Threlfall. 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. Auk 89:789-816.

Nelson, J. B. 1970. The relationship between behaviour and ecology in the Sulidae with reference to other sea birds. Oceanography and Marine Biology, an Annual Review 8:501-574.

Olsthoorn, J. C. M., and J. B. Nelson. 1990. The availability of breeding sites for some British seabirds. Bird Study 37:145-164.

Porter, J. M., and Coulson J. C. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a kittiwake *Rissa tridactyla* colony. Journal of Animal Ecology 56:675-689.

Squibb, R. C., and G. L. Hunt. 1983. A comparison of nesting-ledges used by seabirds on St. George Island. Ecology 64:727-734.

Uspenski, S. M. 1956. The bird bazaars of Novaya Zemlya. Translations of Russian game reports 4 (1958), Canadian Wildlife Service, Queen's Printer, Ottawa, Canada.

Wittenburger, J. F., and G. L. Hunt. 1985. The adaptive significance of coloniality in birds. Avian Biology 3:1-78.

Williams, A. J. 1974. Site preferences and interspecific competition among guillemots *Uria Aalge* (L.) and *Uria lomvia* (L.) on Bear Island. Ornis Scandinavica 5:113-121.

Table 2.1. Characteristics of natural nesting ledges of kittiwakes. Data presented for Red-legged (Red) and Black-legged (Black) Kittiwakes on St. George Island, Alaska.

| | Squibb and Hunt (1983) | | This Study | | | |
|---|---|---|---|---|---|---|
| Measure [a] | Red ($n$ = 86) | Black ($n$ = 70) | Red ($n$ = 255) | Black ($n$ = 203) | Test [b] Statistic | $P$ [c] |
| Ledge Width (cm) | 12 (4.6)[d] | 21 (6.7) | 15.2 (5.0) | 21.4 (8.2) | $Z$ = 9.13 | < 0.001 |
| Ledge Length (cm) | 27 (15.7) | 41 (21.8) | 29.6 (26.9) | 38.8 (23.8) | $Z$ = 7.83 | < 0.001 |
| Ledge Slope (°) | -15 (19.5) | -12 (16.7) | -20.1 (10.9) | -18.9 (10.2) | $Z$ = 0.89 | 0.37, ns |
| Backwall Slope (°) | 87 (10.2) | 89 (9.2) | 79.3 (19.2) | 82.4 (14.7) | $Z$ = 2.14 | 0.03, ns |
| Overhang [e] Presence | 0.63 | 0.27 | 0.51 | 0.26 | $G_1$ = 31.1 | 0.001 |
| Standard [e] Overhang | na | na | 0.47 | 0.34 | $G_1$ = 8.02 | 0.005 |
| Enclosure [f] | na | na | 1.53 | 1.35 | $G_2$ = 11.7 | 0.003 |

[a] see methods section for descriptions of measurements.

[b] $Z$ = Mann-Whitney $U$ test (normal approximation), $G$ = log-likelihood test.

[c] $\alpha$ = 0.05 / 7 comparisons = 0.0071.

[d] $\bar{x}$ and (standard deviation) presented.

[e] no standard deviation computed for this binary variable; value is the proportion of nests with an overhanging backwall.

[f] no standard deviation computed for this categorical variable; value is mean of enclose scores that ranged from 1 (not enclosed) to 3 (fully enclosed).

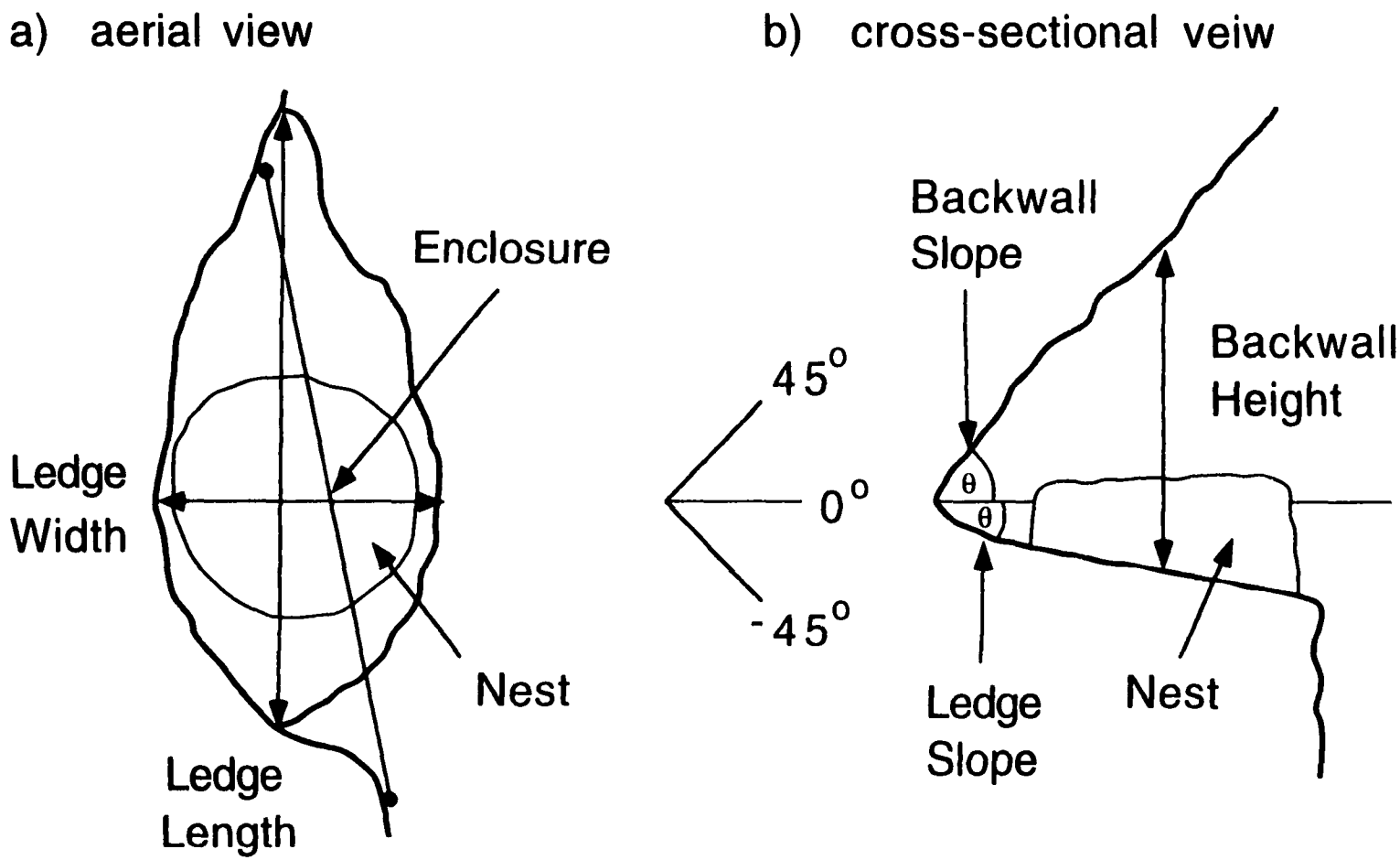


Figure 2.1. Ledge measurements of natural kittiwake nest sites. Aerial (a) and cross-sectional (b) views presented.

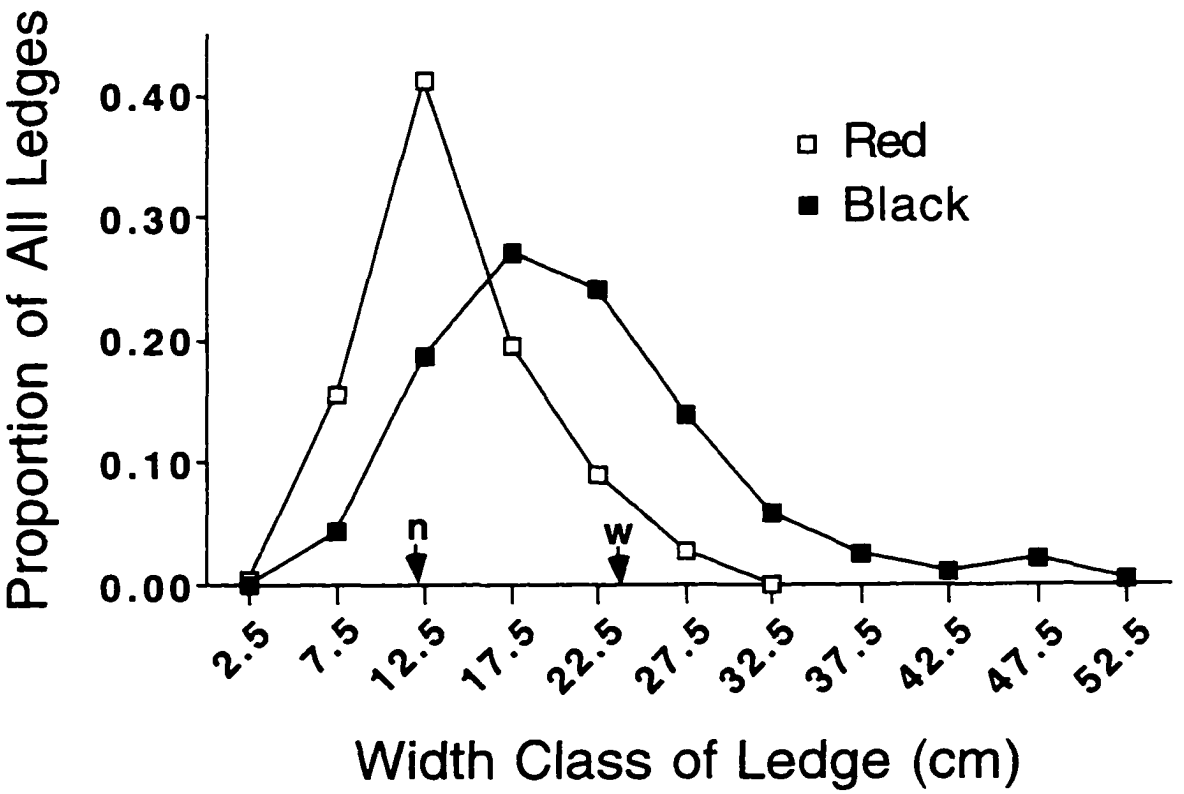


Figure 2.2. Width distributions of natural kittiwake nesting ledges. Relative frequency distributions presented for Red-legged (Red) and Black-legged (Black) Kittiwakes. Values on the x-axis represent midpoints of width classes that span 5 cm each. Arrows above the x-axis indicate the mean widths of narrow (n) and wide (w) artificial ledges.

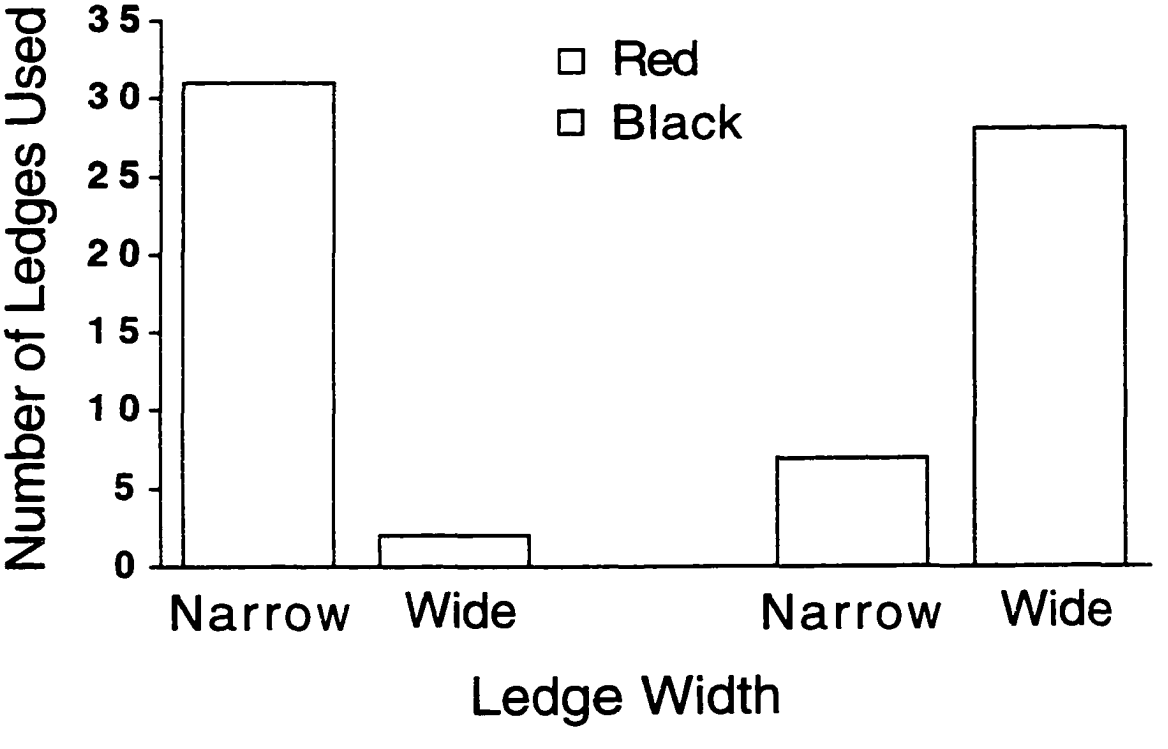


Figure 2.3. Use of narrow and wide artificial ledges by kittiwakes. Relative use of narrow (12.1 cm) and wide (23.3 cm) ledges by Red-legged (Red) and Black-legged (Black) Kittiwakes differed significantly between species and departed significantly from equality within each species.

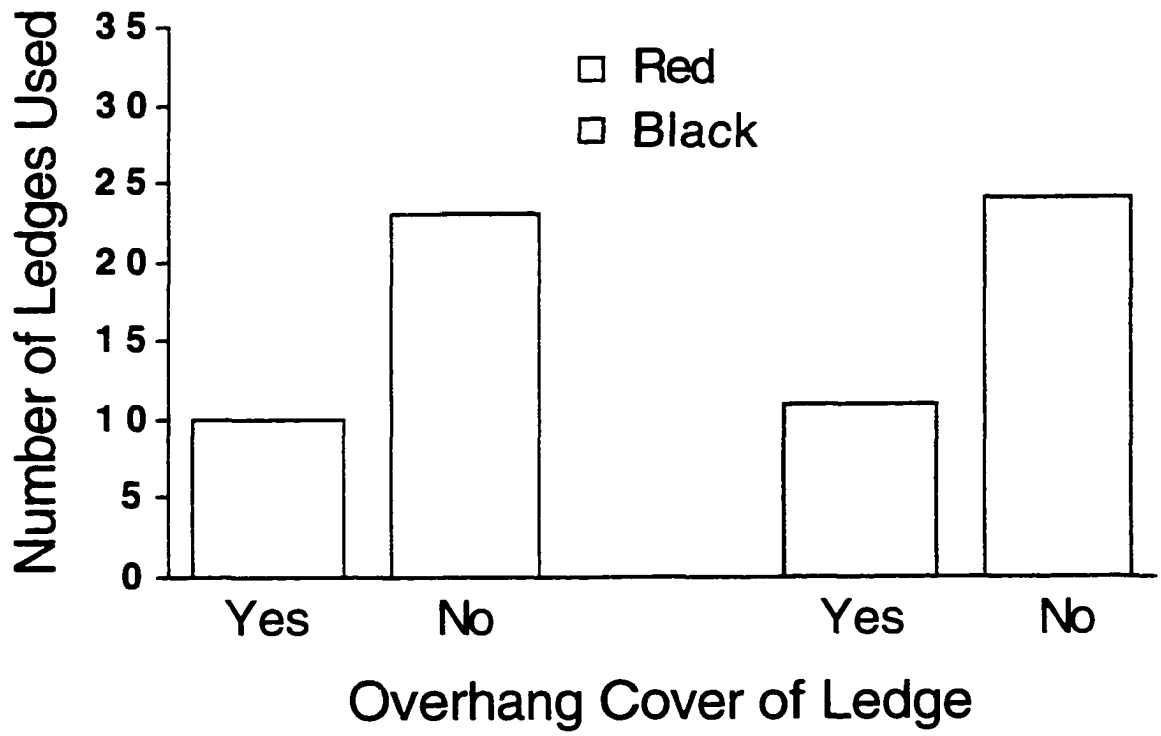


Figure 2.4. Use of artificial ledges with and without overhang cover by kittiwakes. Relative use of ledges with and without overhang cover did not differ between Red-legged (Red) and Black-legged (Black) Kittiwakes but was significantly greater for ledges lacking overhangs for both species.

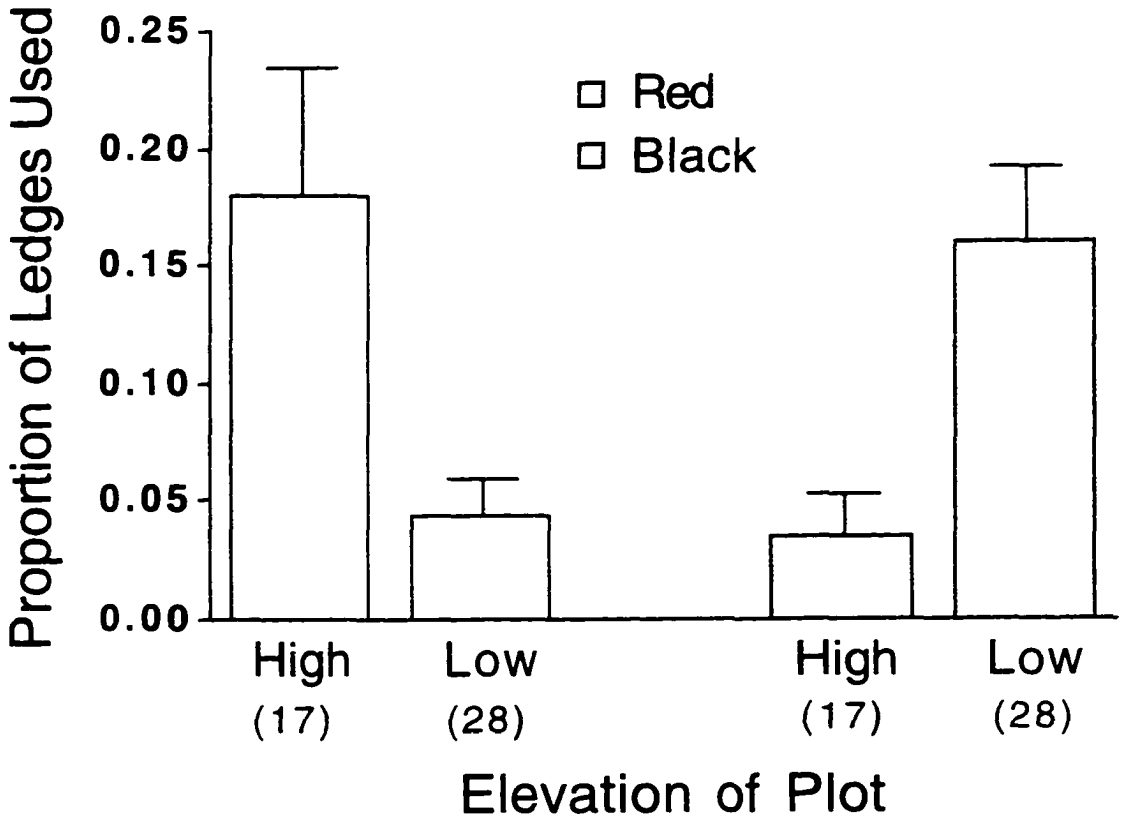


Figure 2.5. Use of artificial ledges at high and low elevations by kittiwakes. The proportion of ledges used by Red-legged (Red) and Black-legged (Black) kittiwakes differed significantly between high-elevation plots (200 - 300 m ASL) and low-elevation plots (3 - 30 m ASL). Means, standard errors, and sample sizes (*n*) are presented.

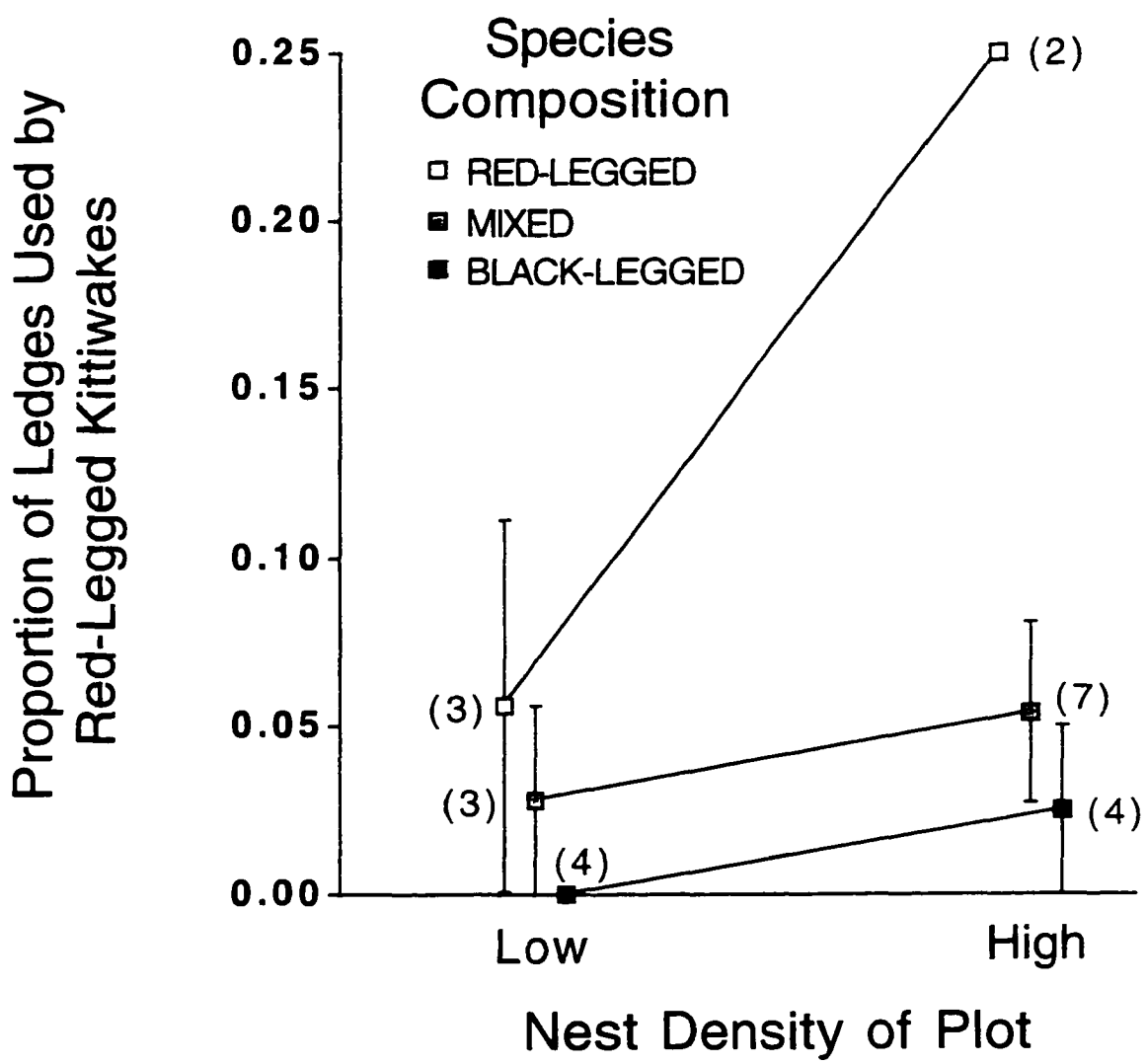


Figure 2.6. Effects of density and species composition of natural nest on use of artificial ledges by Red-legged Kittiwakes. Ledge use was greatest on high-density plots that were red-legged in species composition. Only data from low-elevation plots were considered in this analysis. Means, standard errors, and sample sizes (*n*) are presented.

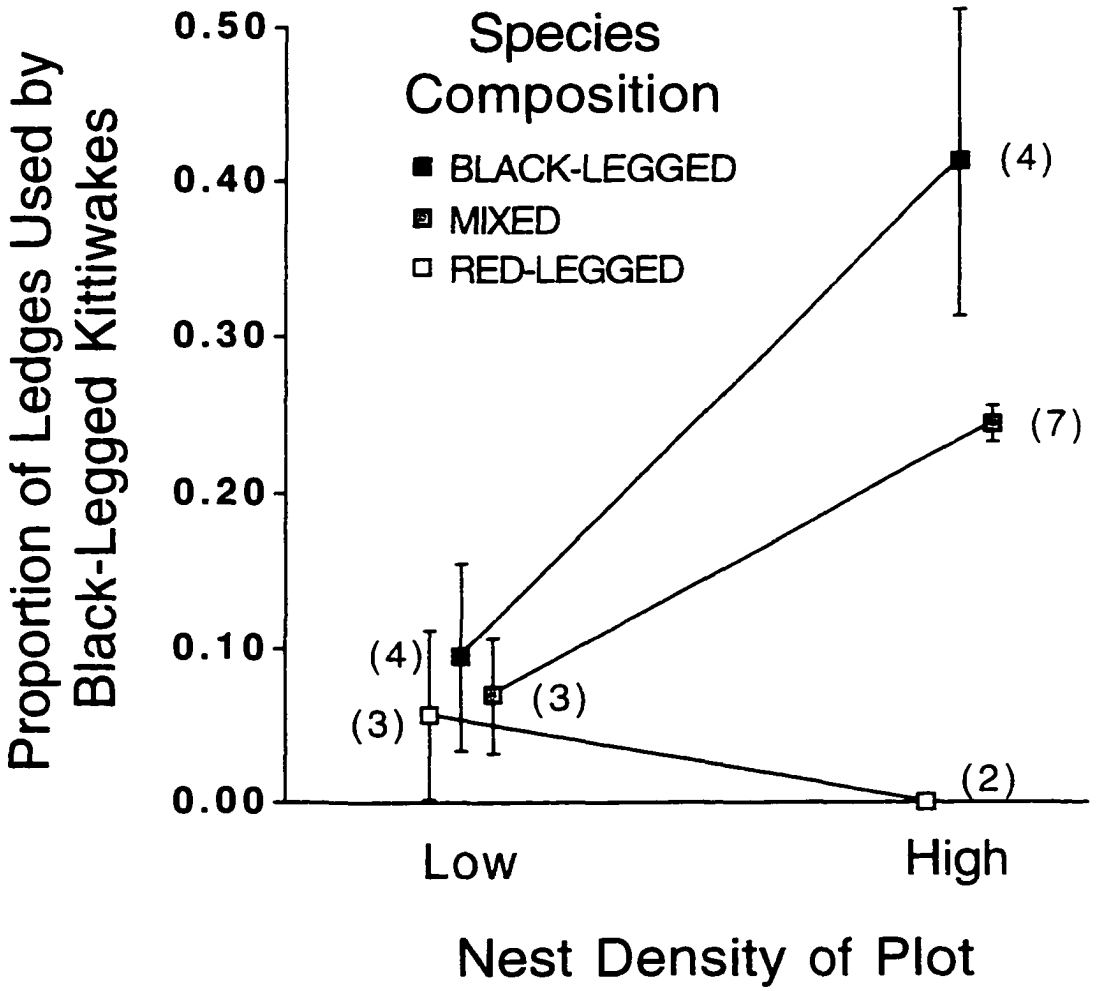


Figure 2.7. Effects of density and species composition of natural nests on use of artificial ledges by Black-legged kittiwakes. Ledge use was greatest on high-density plots that were black-legged in species composition. Only data from low-elevation plots were considered in this analysis. Means, standard errors, and sample sizes (*n*) are presented.

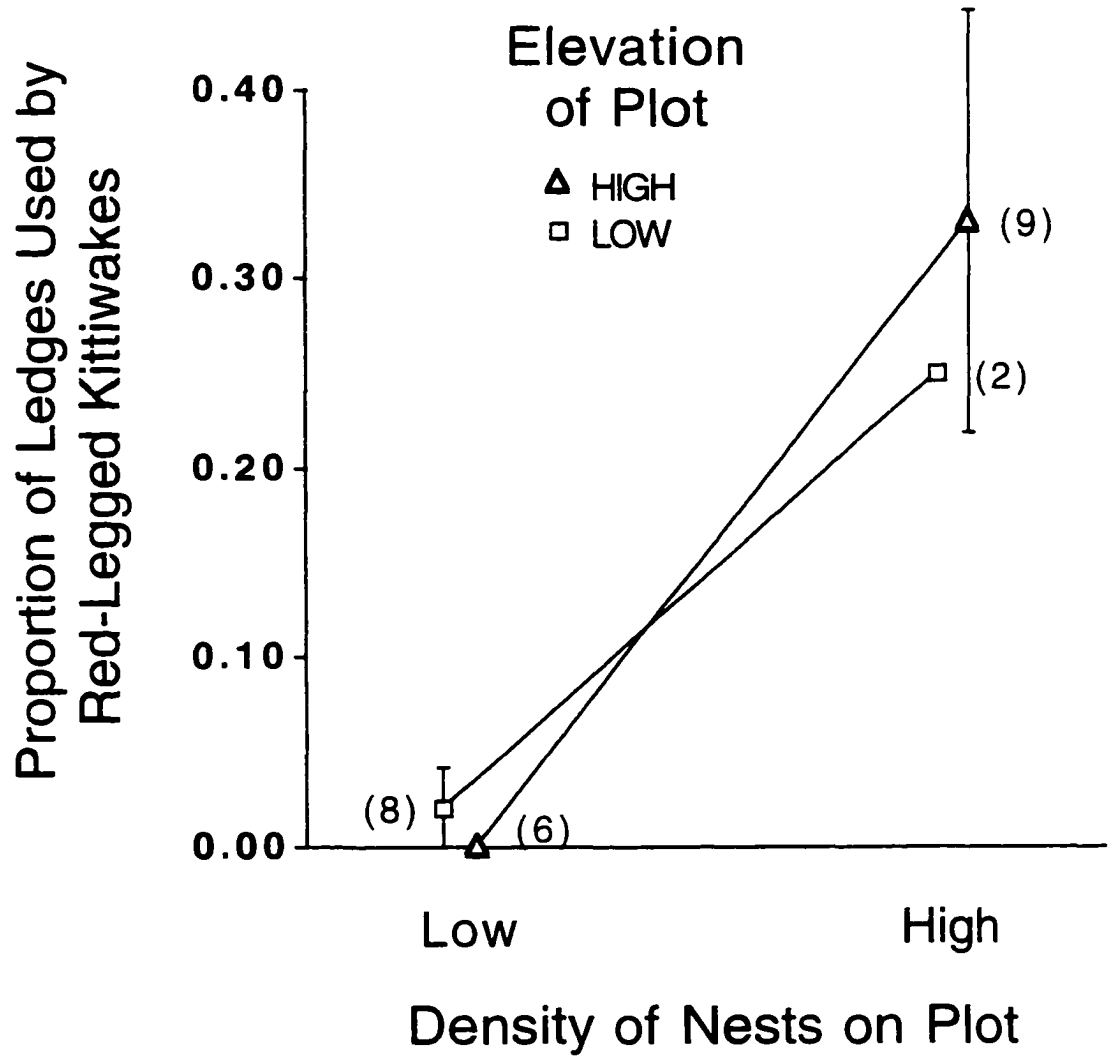


Figure 2.8. Effects of density and elevation on use of artificial ledges by Red-legged Kittiwakes. Ledge use was greater on high-density plots but did not differ between elevations. Only plots that were > 80 % Red-legged Kittiwake in species composition were considered in this analysis. Means, standard errors, and sample sizes (*n*) are indicated.

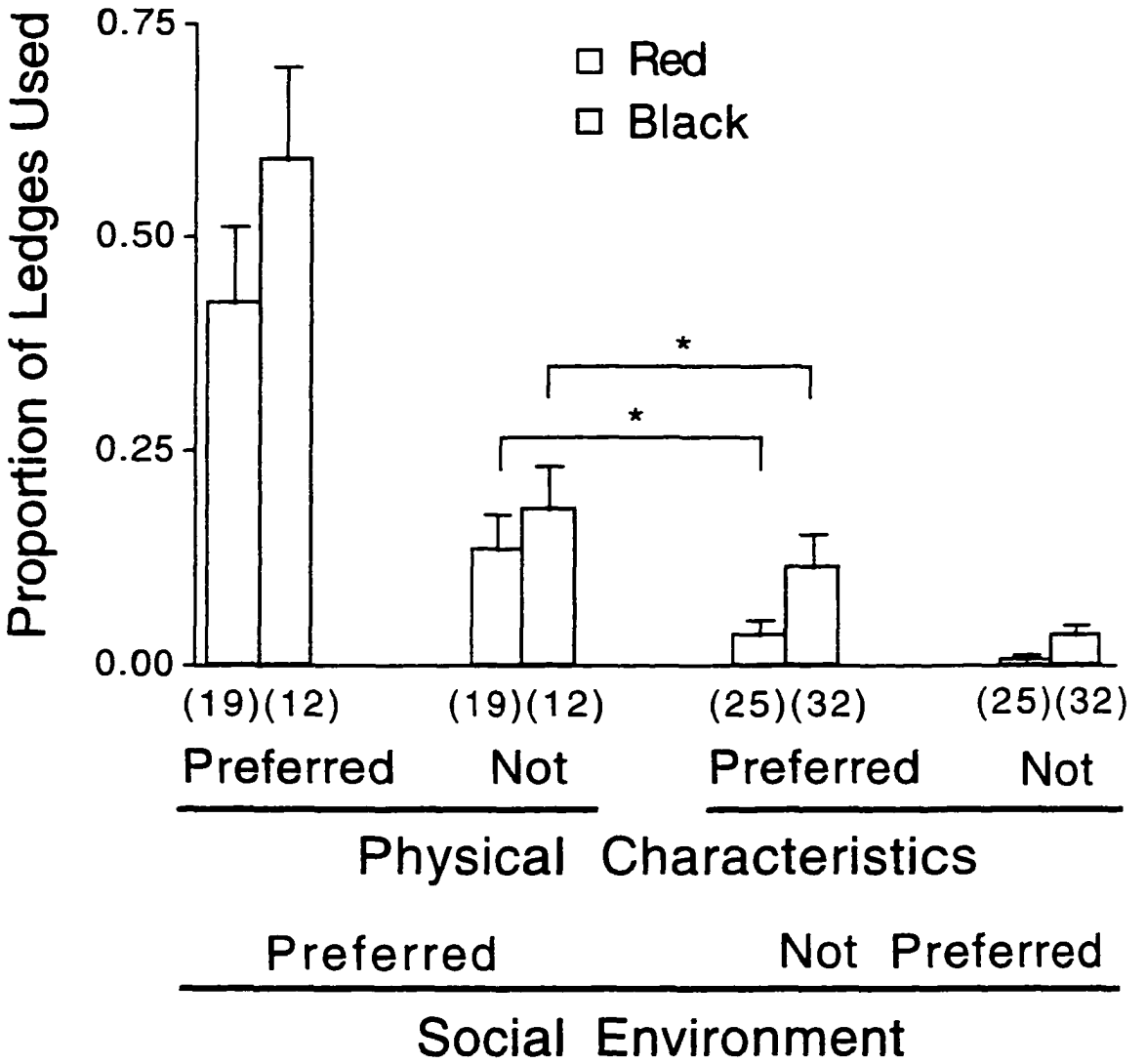


Figure 2.9. Effects of physical characteristics and social environment on use of artificial ledges by kittiwakes. Social characteristics had greater influence on ledge use than did physical characteristics (* = $P < 0.05$) for both Red-legged (Red) and Black-legged (Black) Kittiwakes. Other pairwise comparisons were not performed. Means, standard errors, and sample sizes ($n$) are presented.

# EFFECTS OF WEATHER ON REPRODUCTION AND CHICK GROWTH OF KITTIWAKES[3]

## ABSTRACT

I investigated the effects of weather on the reproduction of Red-legged (*Rissa brevirostris*) and Black-legged Kittiwakes (*R. tridactyla*) on St. George Island, in the Southeastern Bering Sea, in two ways. 1) I used multiple regression models to determine the relationship between each of several reproductive measures of kittiwakes (breeding chronology, laying success, hatching success, fledging success, and overall productivity) and a suite of 11 meteorological and oceanographic variables (air temperature, wind speed, sea ice cover, and sea surface temperature). 2) I evaluated effects of strong winds on the growth of kittiwake chicks in both sheltered and exposed nest sites by comparing chick growth between calm and windy time intervals. Multiple regression models explained between 34% and 68% of interannual variability in kittiwake reproduction and indicated that both species bred earlier and had greater breeding success in summers preceded by cold winters with extensive sea ice cover. These results suggest that winter weather influences kittiwake productivity, indirectly, by affecting oceanographic conditions and the abundance and distribution of kittiwake prey in the vicinity of St. George Island in the following summer. In addition, I found both direct and indirect effects of strong winds on growth rates of kittiwake chicks on St. George Island. Chick growth of both species was negatively affected by direct exposure of nest sites to strong winds, an effect that was most likely due to increased energetic demands of thermoregulation. In addition, effects of wind on chick growth differed significantly between species: wind suppressed the growth of Black-legged Kittiwake chicks relative to that of Red-legged Kittiwake chicks. I propose that the differential response of the two

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species was due to differing effects of wind on foraging efficiency of adults.

## INTRODUCTION

Over the past 20 years, the breeding success of Red-legged (*Rissa brevivostris*) and Black-legged (*R. tridactyla*) Kittiwakes in the North Pacific and the Bering Sea has been generally lower and more variable than that of Black-legged Kittiwakes breeding in the North Atlantic (e.g., Murphy et al. 1991, Hatch et al. 1993). In particular, kittiwakes on St. George Island, in the southeastern Bering Sea, experienced poor productivity and marked population declines during the 1980's (Byrd et al. 1997). The Red-legged Kittiwake, a Bering Sea endemic, is currently a species of concern because more than 80% of its global population breeds on St. George Island (Kildaw 1998), the largest of only four known breeding localities of this species (Byrd et al. 1997). Other upper trophic level consumers in the Bering Sea also have experienced dramatic population reductions over the past two decades (e.g., Steller sea lion, *Eumatopias jubatus*, Merrick et al. 1987; Northern fur seal, *Callorhinus ursinus*, York and Kosloff 1987; harbor seal, *Phoca vitulina*, Pitcher 1990), suggesting that ecosystem-wide changes may have contributed to declines of kittiwake populations on St. George Island. At present, the cause of changing conditions in the Bering Sea is the subject of much debate focused on possible impacts of commercial fisheries and climate change of apex consumers (Springer 1992, Castellini 1993).

A regime-shift from cooler to warmer climatic conditions that occurred in the late 1970's (Neibauer 1988) is one possible explanation for poor reproductive performance of kittiwakes on St. George Island. Weather can influence the reproductive performance of seabirds in several ways. It can have indirect, "bottom-up" effects on prey abundance by altering patterns of ocean primary productivity. The most spectacular example of a bottom-up effect of weather in a marine ecosystem is the "El Nino" phenomena that occurs with a 5-10 year periodicity in equatorial waters of the Eastern Pacific and is responsible for catastrophic reproductive failures and marked population declines of

seabirds and marine mammals (e.g., Schrieber and Schrieber 1989). Weather may also influence foraging conditions for seabirds by affecting the distribution of prey in the water column (Olla and Davis 1990), the roughness of the ocean surface (Dunn 1973, Salt and Willard 1971, Birkhead 1976), and the amount of energy seabirds expend while foraging and commuting between nest sites and feeding areas (Gabrielsen et al. 1987, Furness and Bryant 1996). Lastly, weather can directly affect the reproductive performance of seabirds by exposing eggs, chicks and adult birds to temperature extremes (Gordon 1928, Tuck 1961, Barrett and Runde 1980), or by physically destroying nest sites (Threlfall et al. 1974, Byrd and Tobish 1978).

In this paper I investigate the relationship between weather and reproduction of Red-legged and Black-legged Kittiwakes on St. George Island, Alaska. Kittiwakes are small pelagic gulls that feed by plunge-diving and surface-seizing, and capture prey only within the uppermost 0.5 m of the water column (Byrd and Williams 1993). Kittiwakes, and other species of surface-feeding seabirds, may be especially sensitive to weather conditions because their foraging success is highly dependent not only on prey abundance, but also the vertical distribution of prey in the water column and prey visibility through the air-water interface. Indeed, in Alaskan waters, kittiwakes exhibit greater variability in productivity than do diving species of seabirds (Hatch et al. 1993) which may be related to their limited foraging depth.

Lloyd (1985) examined the relationship between weather and kittiwake reproduction on St. George Island using data from years coincident with the regime shift (1976-1984) and found that reproductive performance of both Red-legged and Black-legged Kittiwakes on St. George Island was negatively correlated with wind speed and precipitation during the breeding season. Using a data set spanning 20 years (1975 - 1995), I re-examined the relationship between the reproduction of kittiwakes on St. George Island and weather conditions in the southeastern Bering Sea by evaluating two predictions of Lloyd's (1985) "bad weather" hypotheses: (1) I tested the prediction that windy, rainy conditions negatively affect kittiwake productivity, by developing multiple

regression models which relate productivity to these and other weather variables; and (2) I tested the prediction that strong winds and rough sea conditions impair the growth of kittiwake chicks, by comparing growth rates of chicks in exposed and sheltered nest sites during calm and windy periods.

## METHODS

*Sources of Data*

I monitored reproductive performance and chick growth of Red-legged and Black-legged Kittiwakes on St. George Island, Alaska, during the summers of 1993 - 1995 on 20 low-elevation plots located near the village of St. George (< 30 m Above Sea Level, ASL) and on 6 high-elevation plots located within the "High Bluff" cliff section (> 200 m ASL). I used a climbing rope or ladder to access reproductive plots every 3-5 days over a three-month period from egg laying through chick fledging and on each visit recorded the developmental status of each nest site. Sites where a level disk of mud/material > 15 cm in diameter and > 5cm thick was constructed before or during the egg laying period and persisted for at least two visits were categorized as "nest attempts". I marked nest and egg numbers on both ends of newly-laid eggs and monitored each egg until either disappearance or the chick's age exceeded 35 days. For broods of two chicks, I assumed that larger chicks were older chicks. All chicks were weighed (± 2 - 5 g) during each nest visit using a Pesola spring scale.

I obtained additional reproductive data for kittiwakes on St. George Island for 1975 - 1995 from several sources: 1975-1978 (Hunt et al. 1981), 1979-81 (Lloyd 1985), 1984 (Johnson and Baker 1985), 1985-1995 (Dragoo and Dragoo 1996). Although study plots and methodologies of these sources were not identical, methods were similar and some study plots were common to all studies. Data were obtained directly from the above sources with the following exceptions: (1) I used reproductive data for 1976 - 1978 as they are presented in Dragoo and Dragoo (1996) rather than in Hunt et al. (1981) because the format of these data in Dragoo and Dragoo (1996) was comparable with data from

later years; (2) I expressed all hatch dates as days since May 31; (3) in two years for which fewer than 10 observations of hatch date were available for a given species of kittiwake, I estimated the mean hatch date by adding the mean incubation period (30 days for Red-legged Kittiwakes and 27 days for Black-legged Kittiwakes; Byrd and Williams 1993) to the mean date of laying of first eggs within each clutch for that species in that year; (4) in seven years for which fewer than 10 observations of both laying and hatching were available for a given species of kittiwake, I estimated the mean date of hatch from the regression relationship observed between mean hatch dates of the two species on St. George I ($\bar{x}$ hatch red = 1.41($\bar{x}$ hatch black) - 19.8, $n$ = 12, $R^2$ = 0.91, $P < 0.001$) or from regression relationships for mean hatch dates of each species between St. George I. and St. Paul I. (Red-legged Kittiwakes; $\bar{x}$ hatch St. George = 1.17($\bar{x}$ hatch St. Paul) - 9.8, $n$ = 8, $R^2$ = 0.86, $P$ = 0.0009) (Black-legged Kittiwakes; $\bar{x}$ hatch St. George = 0.83($\bar{x}$ hatch St. Paul hatch) + 7.3, $n$ = 8, $R^2$ = 0.80, $P$ = 0.007). I established regression equations using data from years with known hatch dates for ≥ 10 nests.

I acquired weather records for 1975 - 1995 from several sources. I obtained monthly, daily, and 3-hourly records of $\bar{x}$ air temperature (AIR), total precipitation (PREC), $\bar{x}$ wind velocity (WIND), resultant wind velocity, and resultant wind direction from Local Climatalogical Records for the National Weather Service (NWS) station located on St. Paul I., approximately 70 km north of St. George I. Resultant wind values reported by the NWS were computed by vector addition of hourly wind measurements of velocity and direction and are in essence "net" wind measurements (reversals in wind direction within the time period cancel each other out). I determined monthly values for NWIND (a measure of the north component of wind speed) by multiplying resultant wind velocity by the cosine of resultant wind direction. NWIND was positive when winds were from the north, negative when winds were from the south, and = 0 when winds were from the east or west. I obtained monthly measures of percent sea ice cover (ICE) for 1975 - 1995 for approximately the eastern half of the Bering Sea (described in Neibauer 1980) from J. Neibauer (unpublished data). From the Climate Research Group of Scripps

Institute of Oceanography. I obtained mean monthly measurements of sea surface temperature and barometric pressure for blocks of 5° latitude and 5° longitude that cover the entire northern Pacific Ocean and southern Bering Sea. In my analyses I use monthly measures of sea surface temperature (SST) for the 5° x 5° block centered over the Pribilof Islands (170° W 55° N). I also computed monthly values of the North Pacific index (NP), a measure of the strength of the Aleutian Low (Barnstron and Livezey 1987), by averaging barometric pressure values, also obtained from the Scripps Institute, over the North Pacific Ocean (160° E-140° W by 30° N-65° N). The Aleutian Low is a dominant weather system in the North Pacific and fluctuations in its strength and position are known to influence temperature and wind conditions in the Bering Sea (Neibauer 1988). Lastly, I obtained monthly values of the Southern Oscillation Index (SOI) from the Climate Diagnostics Bulletin of National Oceanic and Atmospheric Administration (NOAA). The SOI is calculated as the difference between barometric pressure anomalies (departures from the long term average monthly values) of two weather stations in the south Pacific Ocean: Darwin, Australia and Tahiti in the Society Islands. Fluctuations in the SOI are coupled with weather patterns on a global scale and in particular are related to the strength and position of the Aleutian Low in the North Pacific (Neibauer 1988).

*Effects of Weather on Kittiwake Reproduction*

I constructed explanatory models of the relationship between reproductive parameters of kittiwakes and weather variables using a multiple regression approach. I developed regression models for each of the following reproductive parameters for both Red-legged Kittiwakes and Black-legged Kittiwakes:

Hatch Date = mean hatch date for first eggs within clutches

Laying Success = E/N

Hatching Success = C/E

Fledging Success = F/C

Productivity = F/N

Where: N = total number of nest attempts, E = number of nests where ≥ 1 egg was laid, C = number of nests where ≥ 1 chick hatched, and F = number of nests where ≥ 1 chick fledged. Laying and hatching were assumed to have occurred on the midpoint between the date on which the egg or chick was first observed and the date of the previous nest visit. Chicks were considered to have survived to fledging when 27 days old for Red-legged Kittiwakes and 33 days old for Black-legged Kittiwakes (Dragoo and Dragoo 1996). In regression models developed for Black-legged Kittiwakes, I replaced Hatching Success and Fledging Success with "HF Success" (= F/E) because Hatching Success and Fledging Success could not be individually calculated in several years.

I began with an array of 96 weather variables as potential explanatory variables for multiple regression analyses (12 monthly variables for each of 8 weather parameters) and samples of 16 - 20 years of observations for reproductive variables. I initially transformed each weather variable to a centered (mean = 0), "anomaly" distribution by subtracting long-term monthly means from absolute monthly measurements.

I used objective procedures to reduce this pool of candidate weather variables in regression analyses to as few as possible: multiple regression analyses will generate good-fitting models from random "noise" when the number of potential explanatory variables exceeds the sample size and, ideally, the number of potential explanatory variables (weather variables) should not exceed 10 % the number of observations (years)(Neter at al. 1990). I first pooled monthly variables into three "seasons" that corresponded to identifiable stages of the annual cycle of kittiwakes by simply summing anomaly values across months:

Winter = January + February + March (kittiwakes absent from breeding colony)

Spring = April + May (colony attendance, nest building)

Summer = June + July + August (incubating, brood-rearing).

I then deleted weather variables for September - December and was left with 24 (three seasonal measures for each of 8 weather parameters). Throughout this paper I refer to weather variables by concatenating the abbreviation for the weather parameter (AIR,

PREC, WIND, NW, ICE, SST, SOI, NP) and the season (winter, spring, summer).

In multiple regression analyses, variables that are highly correlated are redundant, will mask one another, and will produce unreliable parameter estimates with inflated variances (Neter et al. 1990). I further reduced the number of weather variables and eliminated inter-correlations between them by performing principal component (PC) analyses on 3 suites of highly correlated ($r > .70$) weather variables and replaced each suite with the first principal component of each analysis ($R^2$ values describe the amount of joint variability in the original weather variables that is contained in the first PC axis): the variable PCwinter ($R^2 = 0.92$) replaced AIRwinter and ICEwinter; PCspring ($R^2 = 0.87$) replaced AIRspring, ICEspring, and SSTspring; and PCsummer ($R^2 = 0.86$) replaced AIRsummer and SSTsummer.

Lastly, I dropped 9 of the remaining 20 weather variables on grounds of biological irrelevance. I had initially considered SOI and NP for inclusion in multiple regression analyses because each had the potential to integrate variability observed in other weather variables; however, I dropped SOI and NP because they were only weakly correlated with other weather variables and could not influence kittiwake reproduction directly. I eliminated the variable ICEsummer because during the summer months the ice edge retreats more than 1000 km north of St. George Island into the Chukchi Sea where it does not direclty affect breeding kittiwakes. Lastly, I eliminated the variables WINDwinter and PRECwinter because these variables should not affect physical oceanographic conditions near St. George Island in the following summer.

Having reduced the pool of weather variables to 11, I visually inspected bivariate scatter plots of reproductive parameters and weather variables for non-linearity and outlying data points. Where a scatter plot suggested a curvilinear relationship, I fit linear and quadratic regressions to the data. If the $R^2$ of the quadratic model exceeded 0.36 and improved upon the $R^2$ of the linear model by > 0.2, I added the squared term of the weather variable to the pool of candidate weather variables for that particular reproductive parameter. I screened outlying observations for errors in data entry but

otherwise retained these data points.

For each species, I performed a "best subsets" multiple regression analysis (Neter et al. 1990) for each reproductive parameter using the pool of weather variables developed above as potential independent variables. I used the adjusted $R^2$ criterion to identify the 5 best-fitting regression models for each size class of model containing 1, 2, 3, 4, and 5 weather variables, respectively, and used PRESS scores and Mallow's $C_p$ statistics to select the "best" model. I identified all models with PRESS scores within 15% of the value of the lowest PRESS score and, from this subset of potential models, used $C_p$ scores and Mallow's graphical method to select the "best" model. In short, the best model had the lowest $C_p$ score where $C_p$ first approached $p$, the number of parameters in the regression model, including the intercept term (Neter et al. 1990). For all selected models I performed standard residual analyses for normality and outliers and plotted residuals against each weather variable incorporated in the model.

For several years in which the timing of kittiwake reproduction was exceptionally late (Hatch Date > 29 July), the standard seasonal definitions for spring and summer poorly match pre-breeding and breeding phases of the kittiwake reproductive cycle. Therefore, to investigate the influence of timing of breeding on multiple regression models, I extended the Spring "pre-breeding season" to include June and shifted the Summer (breeding) season to span July - September, because these "seasons" better reflected the breeding chronology of kittiwakes in those years, and compared regression models generated using original and modified seasonal definitions.

*Effects of Wind on Chick Growth Rates*

I evaluated the effects of wind conditions on the growth rate of kittiwake chicks by comparing measurements of growth between windy and calm periods. I defined "storm" events as periods during which mean wind velocities in excess of 25 km/h were sustained for a minimum of 12 hours. In contrast, average wind velocities during "calm" periods in the summer never exceeded 20 km/h. During the summer months, strong

winds were associated with low pressure fronts moving easterly across the southern Bering Sea and typically persisted for 18-36 hr. I recorded the start and stop time of each storm event as well as average wind direction, total precipitation, and average wind velocity for the 12 hr period with the strongest winds.

I determined growth rates for kittiwake chicks in 1993 and 1994 from periodic chick weights by computing daily mass increments for each chick over each interval between successive nest visits. Daily mass increments reflect not only growth over the time interval but also changes in the amount of food in the chick's digestive tract. Although variation in stomach fullness contributes to variability in mass increments, the average mass increment for a sample of chicks over several time intervals represents an unbiased estimate of chick growth. I did not include chick age as a covariate in my analyses because chicks of both kittiwake species exhibited approximately linear growth between 4 and 25 days (Fig. 3.1), and I restricted growth data to this age range in all analyses.

For each chick, I determined the proportion of each interval that was characterized by storm conditions. Intervals that were less than 25% storm were classified as Calm intervals, and intervals that were more than 25% storm were classified as Storm intervals. I used 25% as the classification criterion because it maximized the number of chicks (the sample size) for which growth measurements could be compared between Calm and Storm intervals in both 1993 and 1994. To avoid pseudo-replication, I determined the average growth rate of each chick across all calm and all storm intervals, and performed statistical tests on paired-sample differences in mean growth of individual chicks between calm and storm intervals. Negative differences indicated that chick growth rates were suppressed during storms while positive differences indicated that growth rates were enhanced during storms.

The most severe storms of the nestling period in both 1993 and 1994 were from the north and occurred when most kittiwake chicks were less that 14 days of age. Although all nest sites were located on north-facing cliffs, nests at higher elevations

experienced dense fog almost continually and were exposed to severe updrafts when winds were from the north. At times, updrafts were so strong at High Bluff that adult kittiwakes had difficulty landing at nest sites and were forced to alter their incubating or brooding posture to avoid being physically blown from the nest (pers. obs.). To evaluate the effects of nest exposure on chick growth, I compared chick growth rates between exposed nest sites at the "High Bluff" section of cliff (> 200 m ASL) and more-sheltered nest sites near the village at low elevation (< 30 m ASL).

For each year, I evaluated the effect of storms on chick growth rates by performing a two-factor ANOVA using storm vs. non-storm difference measurements of chick growth with species and nest exposure as factors. I also compared the effects of storms on growth rate of chicks of each species within each treatment (exposed vs. sheltered) within each year, using Wilcoxon tests and applying a Bonferroni adjustment to $P$ values to compensate for these multiple comparisons. These analyses were performed on rank-transformed data because raw difference data did not meet parametric assumptions. All statistical analyses were performed using SAS 6.11 for Windows.

## RESULTS

### *Effects of Weather on Kittiwake Reproduction*

Multiple regression models explained between 34 % and 69 % of the inter-annual variability observed in reproductive variables of both kittiwake species (Table 3.1). The weather variable PCwinter, a measure of air temperature and sea-ice cover during the winter, was the most important factor in regression models for both species (Table 3.1).

For Red-legged Kittiwakes, the relationship between Hatch Date and PCwinter was curvilinear with an $R^2$ of .68, the highest of any regression model examined in this analysis (Table 3.1). Red-legged Kittiwakes bred earliest when the preceding winter was moderately cold and bred later when the winter was warm or extremely cold (Fig. 3.2). In addition, Red-legged Kittiwakes exhibited greater Laying Success, Fledging Success, and Productivity in years preceded by cold winters (PCwinter) and calm springs

(WINDspring), but greater Hatching Success during windy summers (WINDsummer, NWsummer) (Table 3.1).

Black-legged Kittiwakes bred earlier in summers preceded by calm springs (WINDspring) and by strong north winds during the winter (NWINDwinter). Furthermore, reproductive performance was greater in years preceded by cold winters (PCwinter) and calm (NWINDspring), dry (PRECspring) springs (Table 3.1).

Multiple regression models developed using original and modified seasonal definitions were comparable: breeding success was poorly related to weather conditions during the summer breeding season and was positively related to cold conditions in the winter (PCwinter) in both sets of analyses. Although most original and modified "best-fit" regression models included the same weather variables, modified seasonal definitions improved the fit ($R^2$) moderately in 5 of 9 instances.

*Effects of Wind on Chick Growth Rates*

A two-factor ANOVA performed on rank-transformed data indicated that the effect of storms on the growth rate of kittiwake chicks differed significantly between species and between nest sites in exposed vs. sheltered locations in both 1993 (species: $F_{1,111} = 7.3$, $P = 0.008$; exposure: $F_{1,111} = 5.8$, $P = 0.02$) and 1994 (species: $F_{1,102} = 6.6$, $P = 0.01$; exposure: $F_{1,102} = 8.6$, $P = 0.004$; Fig. 3.4), but the species * exposure interaction was not significant in either year (1993: $F_{1,111} = 0.37$, $P = 0.5$; 1994: $F_{1,102}$ 2 = 0.08, $P = 0.8$). Strong winds were associated with reduced growth of Black-legged Kittiwake chicks, relative to Red-legged Kittiwake chicks, and, for both species, were associated with reduced chick growth in exposed vs. sheltered nest sites (Fig. 3.3). Although there were significant effects of species and nest exposure on the response of growth rates of kittiwake chicks to strong winds, in neither year did the mean response of either species in either treatment differ significantly from 0, the null expectation (all $P > 0.05$). Regardless, data for chicks in sheltered nest sites suggest that the growth of Red-legged Kittiwake chicks is enhanced during windy weather while the opposite is true for Black-

legged Kittiwake chicks.

## DISCUSSION

### *Effects of Weather on Kittiwake Reproduction*

My results agree with those of Lloyd (1985) who also found enhanced productivity of kittiwakes in cool, calm, dry summers; however, they suggest indirect rather than direct effects of weather because breeding success was not related to weather conditions during the summer breeding season. In contrast to the "bad weather" hypothesis, reproductive timing and breeding success were better explained by cool, calm, and dry weather conditions during winter and spring periods prior to the breeding season.

Negative relationships between sea surface temperatures and breeding success in seabirds have also been observed in highly productive coastal upwelling systems at lower latitudes (Ainley et al. 1995; Duffy et al. 1984) where cold water, abundant nutrients, and enhanced ocean productivity are associated. Although weather can influence primary production in the southeastern Bering Sea by affecting the temperature profile and post-bloom wind mixing of water overlying the continental shelf (Muench 1983, Sambrotto et al. 1986), and can influence ice-edge productivity prior to the spring bloom (Niebauer et al. 1995), effects of cold winters on ocean productivity are poorly understood. Regardless, parallels between the continental shelf of the Southeastern Bering Sea and coastal upwelling systems are likely superficial because processes regulating primary productivity differ between them.

Other researchers reported correlations between seabird reproduction and weather conditions preceding the breeding season, but found relationships opposite to those observed for kittiwakes on St. George Island. In the eastern Bering Sea, air temperature in May, the month preceding egg-laying, was negatively related to the timing of Black-legged Kittiwake reproduction and was curvilinearly related to the breeding success of both Black-legged Kittiwakes and Common Murres (Uria aalge)(Murphy et al. 1991 and

1986, respectively): kittiwakes and murres had the greatest reproductive success in years with moderately warm springs. Similarly, Common Murres in the Baltic Sea delayed reproduction in years with colder springs (Hedgren 1979) and both murres and kittiwakes at Novaya Zemlya bred later when cold winters preceded the breeding season (Belopol'skii 1957). To summarize, the relationship observed between cooler winter temperatures and both earlier breeding and enhanced reproductive performance for kittiwakes on St. George Island appears to be unique among marine birds in north temperate latitudes.

Birkhead and Harris (1985) suggested that seabirds at high latitudes exhibit greater interannual variability in timing of breeding and compressed pre-laying periods because breeding is constrained by a seasonal weather window of short duration. Faced with these temporal constraints, high latitude seabirds should breed as soon as weather and foraging conditions permit. In contrast, even in cold years with late springs, kittiwakes breeding on St. George Island have at least a 5-month window of ice-free conditions for reproduction.

What then is the ultimate factor regulating the timing of kittiwake reproduction on St. George Island? Lack (1968) viewed the general problem of reproductive timing as one of optimization: in environments where resources are seasonally abundant, birds should overlap the period of peak energetic demand with that of peak resource abundance. Thus, from an evolutionary perspective, kittiwakes on St. George Island should attempt to match their period of greatest energy requirements with the seasonal pulse in prey abundance which is coupled with the annual pulse of primary production (the spring bloom) in the Bering Sea.

For kittiwakes on St. George Island, the time lag between winter weather and the breeding season implies that winter weather has an indirect effect on reproductive timing and success. Weather conditions during the winter can indirectly affect kittiwake reproduction on St. George Island in two ways: 1) by altering foraging conditions prior to the breeding season and thereby affecting the body condition of adult kittiwakes at the

onset of the breeding season, or 2) by altering oceanographic conditions near St. George Island in a manner that affects the abundance or spatial and temporal distribution of kittiwake prey in the following breeding season.

It is difficult to understand how the winter weather conditions on St. George Island could affect winter feeding conditions of kittiwakes because only a small proportion of the kittiwake population is believed to overwinter in the vicinity of St. George Island. Although the winter distribution of kittiwakes that breed in the Bering Sea is poorly known, Red-legged Kittiwakes are believed to winter primarily in the North Pacific (Byrd and Williams 1993) and Black-legged Kittiwakes are thought to be dispersed at low densities (2-3 birds / $km^2$) from the Bering Sea to California (Baird 1994). Only if weather conditions on St. George Island were highly correlated with weather conditions across the general winter range of kittiwakes could the "body condition" hypothesis explain the relationships observed between winter weather and kittiwake reproduction.

A more plausible hypothesis is that winter weather influences kittiwake reproduction by affecting oceanographic conditions and prey abundance near St. George Island in the following summer (Wyllie-Echeverria 1995). Air temperature and sea ice conditions in winter can have a persistent effect on oceanographic conditions by altering the temperature and salinity of continental shelf waters of the Bering Sea. During the winter, sea ice is continually formed in polynyas located along the southern margins of land masses in the northern Bering Sea and is displaced southwards by north winds where it encounters warmer water and melts (Pease 1980). Since sea ice is approximately 50% less saline than the water from which it freezes, the net effect of the southward movement of ice in the Bering Sea is a cooling and freshening of surface waters overlying the continental shelf (Muench 1983, Schumacher et al. 1979). Furthermore, cold, saline residual water from ice formation in polynyas collects in the middle-shelf domain of the Bering Sea (waters 50m - 100m deep, Fig. 3.4) and forms the "cold pool", an oceanographic feature that persists throughout summer (Takenouti and Ohtaini 1974). In

extensive ice years, the cold pool extends throughout the middle shelf domain (from the Gulf of Anadyr in the western Bering Sea to Bristol Bay in the east) while in light ice years the cold pool is restricted to the western half of the Bering Sea shelf (Fig. 3.4).

Residual effects of winter sea ice conditions on the marine ecosystem in the vicinity of St. George Island are potentially many-fold. Temperature and salinity of continental shelf water can affect ocean productivity in the southeastern Bering Sea by affecting the timing of the spring bloom, the location and structure of hydrographic fronts (Schumacher et al. 1979, Coyle and Cooney 1993), and vertical and cross-shelf movements of nutrients via energy inputs from the wind, and tides (Sambrotto et al. 1985). Furthermore, Wyllie-Echeverria (1995) proposed that the areal extent of the cold pool affects spawning and feeding distributions of walleye pollock (*Theragra chalcogramma*), an important prey species for seabirds and marine mammals in the southeastern Bering Sea, because pollock are thermally excluded from the cold pool and may become concentrated in the outer shelf domain (100m - 200m) in heavy ice years. Thus, through the action of all these processes, winter weather can indirectly affect ocean productivity and the abundance and distribution of seabird prey in the vicinity of St. George Island in the following summer.

*Effects of Wind on Chick Growth Rates*

Significant differences between species and effects of nest exposure on growth rates of kittiwake chicks suggest both direct and indirect effects of strong winds on chick growth. I propose that poor growth of chicks exposed to damp, windy conditions was a consequence of increased energetic demands of thermoregulation. Other studies found that wetting compromised the thermoregulatory ability of young Black-legged Kittiwake (Barrett 1978) and Dovekie (*Alle alle*) chicks (Konarzewski and Taylor 1989) and that thermal stress reduced the growth rate of Black-legged Kittiwake chicks (Barrett and Runde 1980).

In addition, differential effects of wind on chick growth rates of the two kittiwake

species suggests indirect effects of wind on provisioning rates of adult kittiwakes. Chick growth in sheltered nest sites suggest that Red-legged Kittiwakes are better able to provision their young during windy conditions while the opposite is true of Black-legged Kittiwakes; however, these patterns are not significant. Other studies indicated that wind elevates the energetic costs of foraging for Black-legged Kittiwakes (Gabrielsen et al. 1987) and that surface-feeding seabirds foraged less efficiently and provisioned chicks at lower rates when winds were strong and sea-surface conditions rough (Dunn 1973, Salt and Willard 1971, Braun and Hunt 1983, Konarzewski and Taylor 1989). Although wind may differentially effect the flight energetics of the two kittiwake species because their flight characteristics differ slightly, I propose that wind has opposite effects on chick growth of the two species because it differentially affects foraging efficiency by affecting the vulnerability of their respective prey.

Perhaps the most biologically important difference between Red-legged and Black-legged Kittiwakes is diet. While Red-legged Kittiwakes specialise on a diet of energy-rich myctophids (Schneider and Hunt 1984, Dragoo 1991, Lance 1996), Black-legged Kittiwakes are more generalist foragers that prey on juvenile (age 0) walleye pollock and a variety of other forage fishes. Differences in diet between the two species are associated with interspecific differences in foraging behavior (both temporal and spatial, Hunt et al.1981), rates of chick provisioning (Lance 1996), morphology (Storer 1987), and breeding distributions (Schneider and Hunt 1984, Springer 1991). Myctophids are energy-rich mesopelagic fishes that are widespread in deep oceanic waters and exhibit diurnal vertical migrations: they spend the day at depth (300 - 400 m) but concentrate at the ocean surface at night to feed on vertically migrating zooplankton (Adams 1979). To encounter myctophids, Red-legged Kittiwakes on St. George Island must forage during the night at or beyond the continental shelf break 30+ km to the south of the island (Fig. 3.4).

The positive effect of wind on the growth of Red-legged Kittiwake chicks suggests that wind in some way improves the nocturnal foraging efficiency of adult Red-

legged Kittiwakes on their myctophid prey: foraging kittiwakes might use the wind to canvas a larger foraging area and thereby increase their encounter rate with myctophids or wind might affect the vertical distribution or vulnerability of myctophids. Perhaps wind and rough sea-surface conditions tumble Myctophids, exposing rows of bioluminescent photophores, which are ventrally-located (Adams 1979), to aerial predators. Although it is presently unclear why the two kittiwake species differ in their response to wind, the foraging efficiency hypothesis can easily be tested by measuring and comparing interspecific rates of food delivery to chicks during calm and windy weather.

To summarize, although Lloyd's (1985) "bad weather" hypothesis correctly predicted reduced growth rates of kittiwake chicks in exposed vs. sheltered nest sites, it does not explain enhanced growth of Red-legged Kittiwake chicks during periods of strong winds. In addition, results of multiple regression analyses contradict the "bad weather" hypothesis: kittiwake breeding success was poorly related to weather conditions during the breeding season and was better explained by indirect effects of winter weather on food web development and on the abundance and distribution of prey in the following summer. Although the "cold pool" hypothesis might explain the connection between winter weather and kittiwake breeding success, further research is required to better understand both direct and indirect effects of weather on the abundance, distribution, and vulnerability of kittiwake prey.

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## LITERATURE CITED

Adams, A. E., Jr. 1979. The food habits, age, and growth of three midwater fishes (*Stenobrachius leucopsarus*, *Stenobrachius nannochir* and *Leuroglossus schidti*) from the southeastern Bering Sea. M.S. dissertation, University of Alaska, Fairbanks.

Ainley, D. G., W. J. Sydeman, and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecology Progress Series 118:69-79.

Baird, P. H. 1994. Black-legged Kittiwake (*Rissa tridactyla*). Pages 1-28 *in* The birds of North America, no. 92 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences of Philadelphia and American Ornithologists' Union, Philadelphia, Pennsylvania, USA.

Barnstron, A., and R. E. Livezey. 1987. Classification, seasonality and persistence of low-frequency circulation patterns. Monthly Weather Review 115:1083-1126.

Barrett, R. T. 1978. Adult body temperature and the developement of endothermy in the kittiwake (*Rissa tridactyla*). Astarte 11:113-116.

Barrett, R. T., and A. J. Runde. 1980. Growth and survival of nestling kittiwakes *Rissa tridactyla* in Norway. Ornis Scandinavica 11:228-235.

Belopol'skii, L. O. 1957. Ecology of sea colony birds of the Barents Sea. Israel Program for Scientific Translations (1961), Jerusalem, Israel.

Birkhead, T. R. 1976. Effects of sea conditions on rates at which Guillemots feed chicks. British Birds 69:493-494.

Birkhead, T. R., and M. P. Harris. 1985. Ecological adaptations for breeding in Atlantic Alcidae. Pages 205-231 *in* The Atlantic Alcidae (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, London, England.

Braun, B. M., and G. L. Hunt, Jr. 1983. Brood reduction in Black-legged Kittiwakes. Auk. 100:469-476.

Byrd, G. V., and T. G. Tobish. 1978. Wind-caused mortality in a kittiwake colony at Buldir Island, Alaska. Murrelet 59:37.

Byrd, G. V., and J. C. Williams. 1993. Red-legged Kittiwake (*Rissa brevirostris*). Pages 1-11 *in* The birds of North America, no. 60 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences of Philadelphia and American Ornithologists' Union, Philadelphia, Pennsylvania, USA.

Byrd, G. V., Williams, J. C., Artukhin, Y. B., Vyatkin, P. S. 1997. Trends in populations of Red-legged Kittiwake (*Rissa brevirostris*), a Bering Sea endemic. Bird Conservation International 7:167-180.

Castellini, M. 1993. Report of the Marine Mammal Working Group. Pages 4 - 13 *in* Is it food? Alaska Sea Grant College Program, Fairbanks, Alaska, USA.

Coyle, K. O., and R. T. Cooney. 1993. Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea. Continental Shelf Research 13:803-827.

Dragoo, D. E. 1991. Food habits and productivity of kittiwakes and murres at St. George Island, Alaska. M.S. dissertation, University of Alaska, Fairbanks.

Dragoo, D. E., and B. K. Dragoo. 1996. Results of productivity monitoring of kittiwakes and murres at St. George Island, Alaska, in 1995. U. S. Fish and Wildlife Service, Homer, Alaska, USA.

Duffy, D. C., A. Berruti, R. M. Randall, and J. Cooper. 1984. Effects of the 1982-3 warm water event on the breeding of South African seabirds. South African Journal of Science 80:65-69.

Dunn, E. K. 1973. Changes in fishing ability of terns associated with windspeed and sea surface conditions. Nature 244:520-521.

Furness, R. W., and D. M. Bryant. 1996. Effect of wind on field metabolic rates of breeding Northern Fulmars. Ecology 77:1181-1188.

Gabrielsen, G. W., F. Mehlum, and K. A. Nagy. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes. Condor 89:126-132.

Gordon, S. 1928. Effect of bad weather on young kittiwakes in Skye. British Birds 22:116.

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt. 1993. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. Pages 140-153 *in* The status, ecology, and conservation of marine birds in the north Pacific (K. T. Briggs, K. H. Morgan, and D. Seigel-Causey, Eds.). Canadian Wildlife Service Special Publication. Ottawa, Canada.

Hedgren, S. 1979. Seasonal variation in fledging weight of guillemots *Uria aalge*. Ibis 121:356-361.

Hunt, G. L. Jr., Z. Eppley, B. Burgeson, and R. Squibb. 1981. Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands, 1975-1979. Environmental Assessment of the Alaskan Continental Shelf, Final Reports of the Principal Investigators. National Oceanic and Atmospheric Administration Environmental Research Laboratory, Boulder, Colorado 12:1-258.

Johnson, S. R., and J. S. Baker. 1985. Productivity studies. Pages 191-256 *in* Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, Bering Sea, Alaska (S. R. Johnson, Ed.). LGL Ecological Research Associates, Inc., Bryant, Texas, USA.

Kildaw, S. D. 1998. Population status and patterns of distribution and productivity of kittiwakes on St. George Island, Alaska. Ph. D. thesis. University of Alaska Fairbanks, Fairbanks Alaska, USA.

Konarzewski, M. K., and J. R. E. Taylor. 1989. The influence of weather conditions on growth of Little Auk *Alle alle* chicks. Ornis Scandinavica 20:112-116.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.

Lance, B. K. 1996. Diet and nestling growth of Red-legged and Black-legged Kittiwakes: an interspecies cross-fostering experiment. M. S. thesis. University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Lloyd, D. S. 1985. Breeding performance of kittiwakes and murres in relation to oceanographic and meteorologic conditions across the shelf of the southeastern Bering Sea. M.S. dissertation. University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Merrick, R. L., T. R. Loughlin, and D. G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumatopias jubatus*, in Alaska, 1956-86. Fisheries Bulletin 85:351-365.

Muench, R. D. 1983. Mesoscale oceanographic features associated with the central Bering Sea ice edge: February-March 1981. Journal of Geophysical Research 88:2715-2722.

Murphy, E. C., A. M. Springer, and D. G. Roseneau. 1986. Population status of common guillemots at a colony in western Alaska: results and simulations. Ibis 128:348-363.

Murphy, E. C., A. M. Springer, and D. G. Roseneau. 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactlya* L.) at a colony in western Alaska. Journal of Animal Ecology. 60:515-534.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models. Third edition. Irwin, Burr Ridge, Illinois.

Niebauer, H. J. 1980. Sea ice and temperature variability in the eastern Bering Sea and the realation to atmospheric fluctuations. Journal of Geophysical Research. 85:7507-7515.

Niebauer, H. J. 1988. Effects of El Nino-Southern Oscillation and Northern Pacific weather patterns on interannual variability in the subarctic Bering Sea. Journal of Geophysical Research 93:5051-5068.

Niebauer, H. J., V. Alexander, and S. M. Henrichs. 1995. A time-series study of the

spring bloom at the Bering Sea ice edge I. Physical processes, chlorophyll and nutrient chemistry. Continental Shelf Research 15:1859-1877.

Olla, B. L., and M. W. Davis. 1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Marine Ecology Progress Series 63:105-112.

Pease, C. H. 1980. Eastern Bering Sea ice processes. Monthly Weather Review 108:2015-2023.

Pitcher, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulana richardsi*, on Tugidak Island, Gulf of Alaska. Marine Mammal Science 6:121-134.

Salt, G. W., and D. E. Willard. 1971. Hunting behavior and success of Forster's Tern. Ecology 52:989-998.

Sambrotto, R. N., H. J. Niebauer, J. J. Goering, and R. L. Iverson. 1986. Relationships among vertical nixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeastern Bering Sea middle shelf. Continental Shelf Research 5:161-198.

Schneider, D., and G. L. Hunt, Jr. 1984. A comparison of seabird diets and foraging distributions around the Pribilof Islands, Alaska. Pages 86-95 *in* Marine birds: their feeding ecology and commercial fisheries relationships (D. N. Nettleship, G. A. Sanger and P.F. Springer, Eds.). Canadian Wildlife Service Special Publication, Ottawa, Canada.

Schrieber, E. A., and R.W. Schrieber. 1989. Insights into seabird ecology from a global 'natural experiment'. National Geographic Research 5:64-81.

Schumacher, J. D., T. H. Kinder, D. J. Pashinski, and R. L. Charnell. 1979. A structural front over the continental shelf of the eastern Bering Sea. Journal of Physical Oceanography 9:79-87.

Springer, A. M. 1991. Seabird distribution as related to food webs and the environment: Examples from the north Pacific ocean. Occasional paper No. 68, Canadian Wildlife Service. Ottawa, Canada.

Springer, A. M 1992. Walleye pollock in the North Pacific - how much difference do they really make? Fisheries Oceanography 1:80-96.

Storer, R. W. 1987. The possible significance of large eyes in the Red-legged Kittiwake. Condor 89:192-194.

Takenouti, A. Y., and K. Ohtaini. 1974. Currents and water masses in the Bering Sea: a review of Japanese work. pp.39-57. *in*: Oceanography of the Bering Sea with emphasis on renewable resources (D. W. Hood and E. J. Kelley, Eds.). Occasional Publication No.2., Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska.

Threlfall, W., E. Eveleigh, and J. E. Maunder. 1974. Seabird mortality in a storm. Auk 91:846-849.

Tuck, L. M. 1961. The murres: their distribution, populations and biology - a study of the genus *Uria*. Canadian Wildlife Service Monograph Series, No. 1., Ottawa, Canada.

Wiley-Echeverria, T. 1995. Seasonal sea ice, the cold pool and gadid distribution on the Bering Sea shelf. Ph.D. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

York, A. E., and P. Kozloff. 1987. On the estimation of the numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980-86. Fisheries Bulletin 85:367-375.

Table 3.1. Multiple regression models relating several measures of kittiwake reproduction to weather.

| n | $r^2$ | Models for reproductive measures of Red-legged Kittiwakes | | | | | |
|---|---|---|---|---|---|---|---|
| 18 | 0.68 | Hatch Date | = | + 47 | + 3.3 (PCwinter$^2$) | + 5.1 (PCwinter) | |
| 17 | 0.54 | Laying Success | = | + 0.68 | - 0.16 (PCwinter) | - 0.067 (PCwinter$^2$) | |
| 17 | 0.36 | Hatch Success | = | + 0.58 | + 0.024 (WINDsummer) | + 0 027 (NWINDsummer) | |
| 16 | 0.51 | Fledge Success | = | + 0.67 | - 0.089 (PCwinter) | - 0.017 (WINDspring) | |
| 20 | 0.39 | Productivity | = | + 0.26 | - 0.072 (PCwinter) | - 0.014 (WINDspring) | |

| n | $r^2$ | Models for reproductive measures of Black-legged Kittiwakes | | | | | |
|---|---|---|---|---|---|---|---|
| 18 | 0.48 | Hatch Date | = | + 51 | + 0.84 (WINDspring) | - 0.69 (NWINDwinter) | |
| 16 | 0.34 | Laying Success | = | + 0.57 | - 0.34 (PCwinter) | - 0.0050 (PRECspring) | |
| 16 | 0.56 | H-F Success | = | + 0 31 | - 0.12 (PCwinter) | - 0.058 (NWINDspring) | - 0.0050 (PRECspring) |
| 19 | 0.36 | Productivity | = | + 0.24 | - 0.094 (PCwinter) | - 0.021 (NWINDspring) | - 0.023 (NWsummer) |

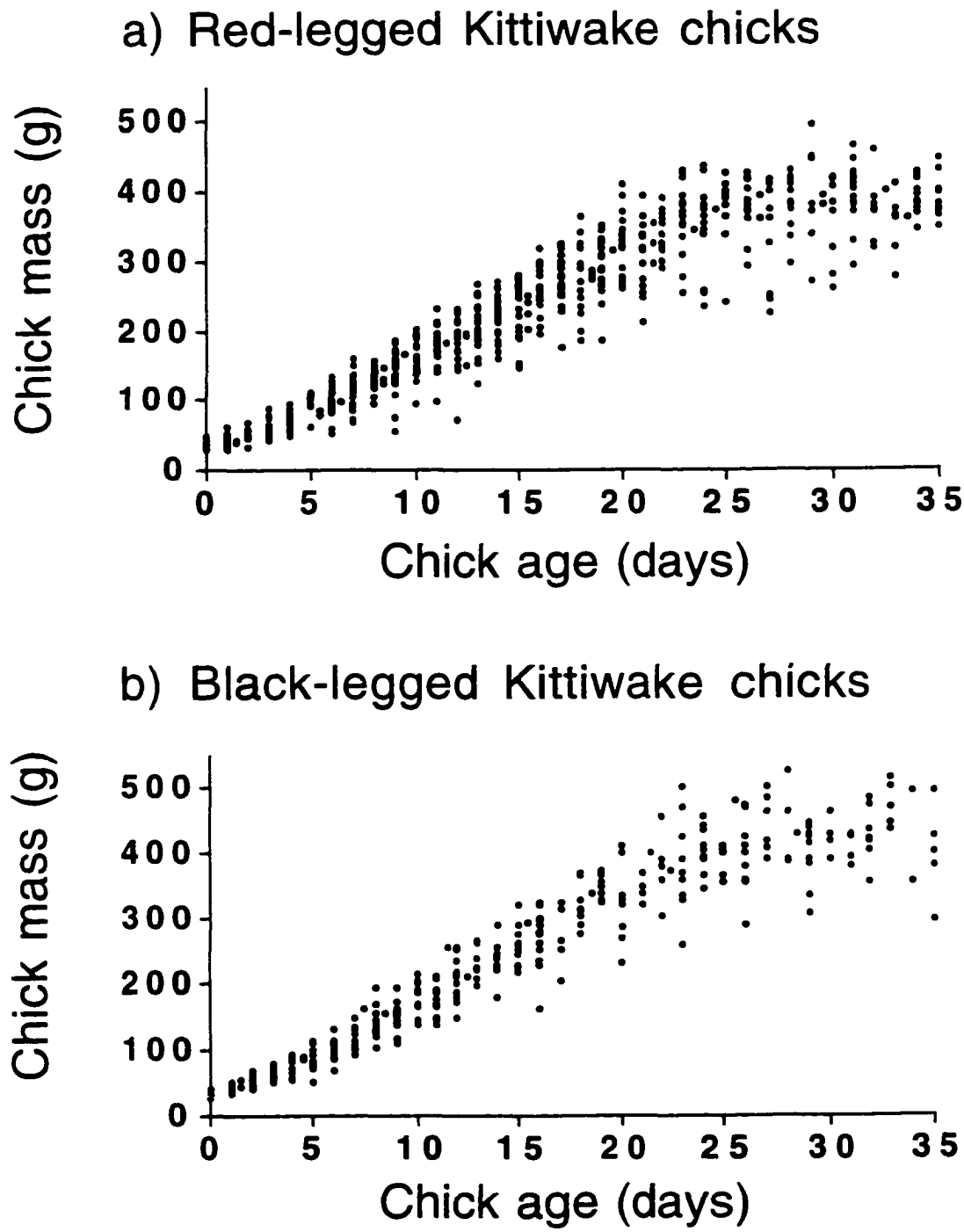


Figure 3.1. Growth trajectories for kittiwake chicks in 1993. Growth rates for Red-legged (a) and Black-legged (b) Kittiwakes were approximately linear between 4 and 25 days.

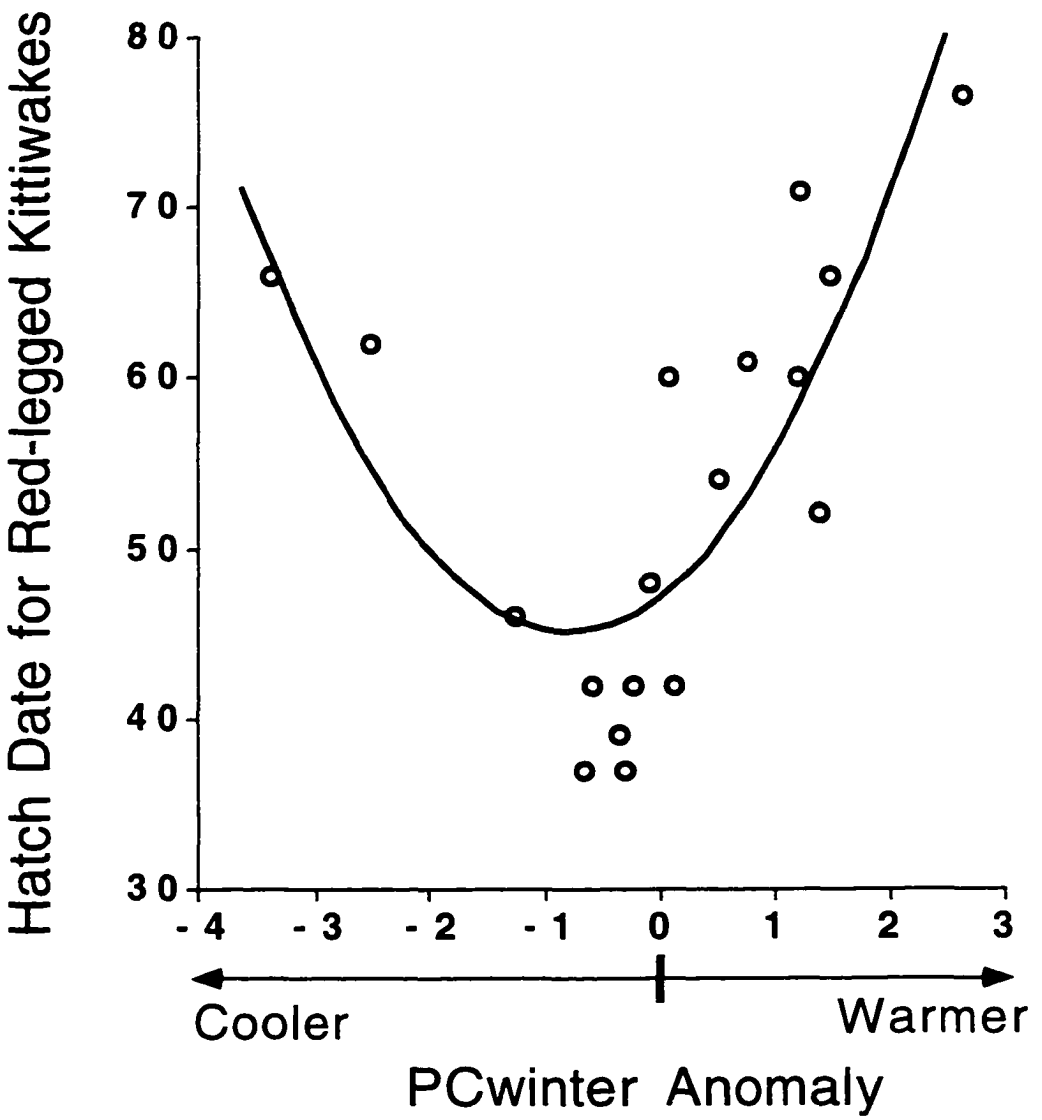


Figure 3.2. Mean hatch date of Red-legged Kittiwakes vs PCwinter. The relationship between hatch date and PCwinter (the first principal component of air temperature and sea ice conditions in winter) is curvilinear: kittiwakes bred earliest in moderately cold years and later in both warmer and extremely cold years.

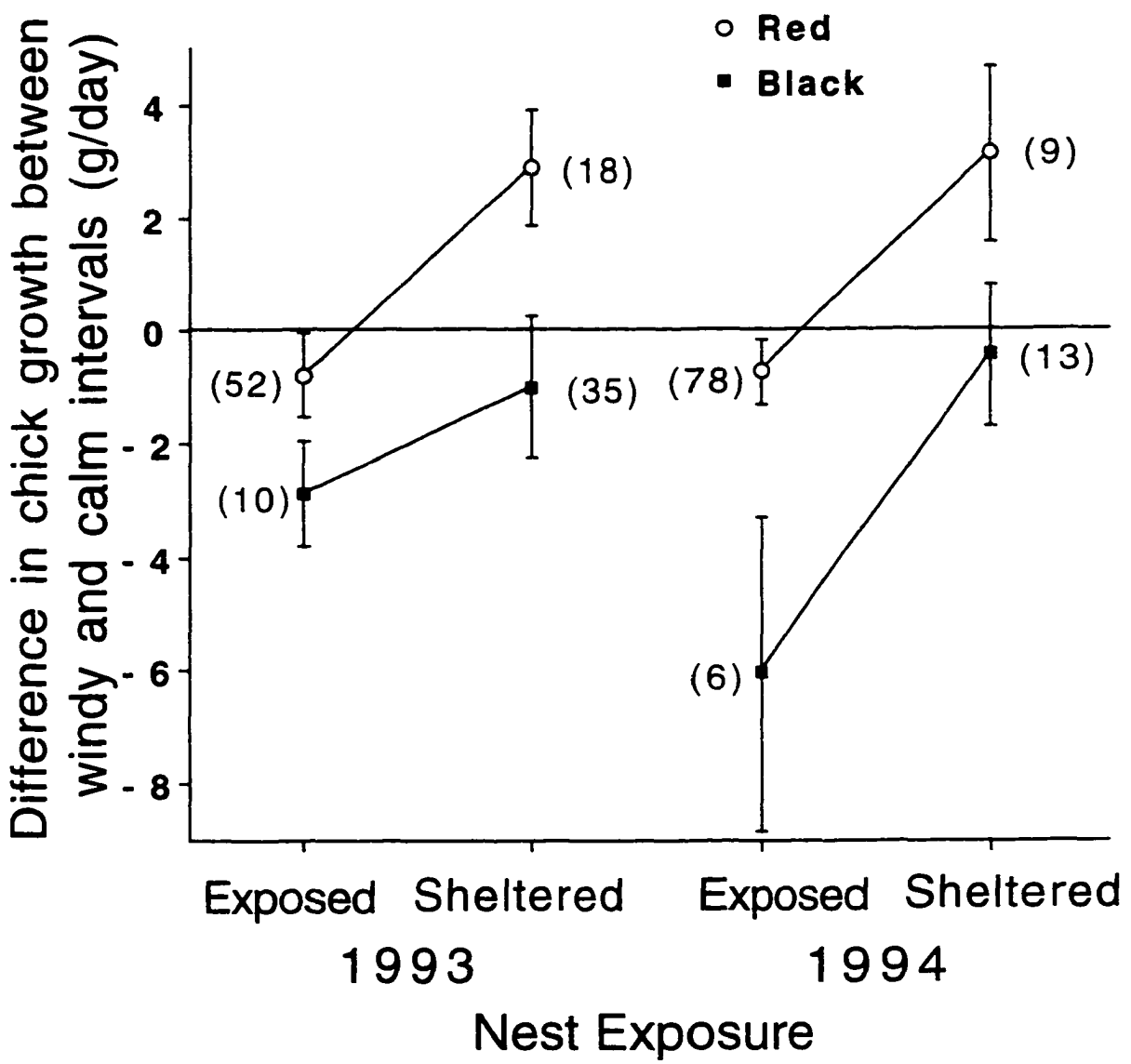


Figure 3.3. Effects of strong winds on growth rates of kittiwake chicks. Effects of wind differed significantly between Red-legged (Red) and Black-legged (Black) kittiwake chicks and between chicks in exposed vs. sheltered nest sites. Means, standard errors, and sample sizes (*n*) are presented.

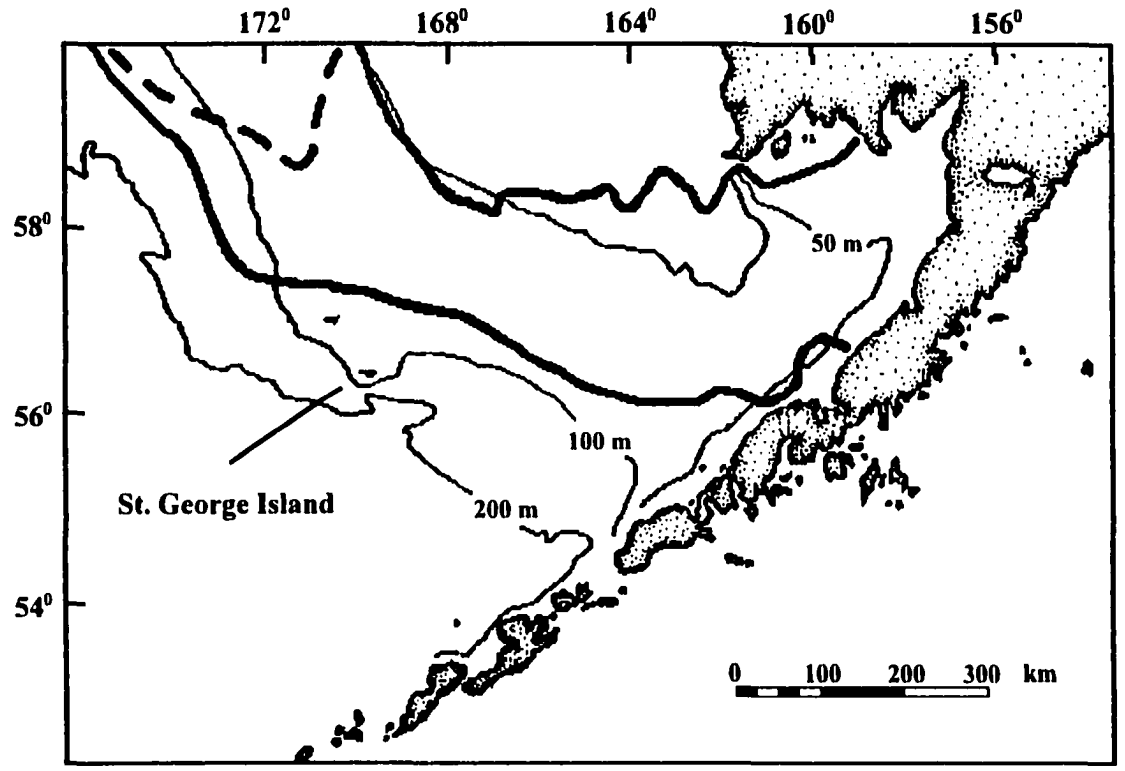


Fig. 3.4. The locations of St. George Island and the "cold pool". Minimum and maximum extents of the "cold pool" in the "middle domain" of the continental shelf of the Bering Sea (50m - 100m depth contours) are indicated by dashed and solid lines, respectively. The continental shelf break is indicated by the 200m depth contour located south of St. George Island.

# WITHIN-COLONY VARIABILITY IN KITTIWAKE PRODUCTIVITY: BIRD QUALITY OR INFORMATION NEIGHBORHOODS? [4]

## ABSTRACT

We documented two patterns of within-colony variability in reproductive success of red-legged (Rissa brevirostris) and black-legged (R. tridactyla) kittiwakes on St. George Island. Productivity was greater within high-density plots located in high-elevation areas (the "High Bluff" effect) and differed significantly among plots with similar social and physical characteristics within each area (the "Within Area" effect). Neither of these patterns was caused by localized effects of food availability, predators, or weather: the three factors most often invoked to explain reproductive variability within colonies, among colonies, and among years. Although lower prevalence of ectoparasites (ticks) potentially explains greater productivity at high elevations, ticks can not explain enhanced productivity of high-density plots or Within-Area variability in productivity. Furthermore, within-colony variability is explained neither by "information center" or "social facilitation" hypotheses. In contrast, the "bird quality" hypothesis may account for greater productivity within high-density plots and variability among high-density plots at high-elevation; however, it can not explain variability within lower-density, lower-elevation, plots or the high productivity of black-legged kittiwakes within high-elevation plots. Therefore, we propose the "information neighborhood" hypothesis to explain spatial clustering of successful and failed nests within plots. Colonial breeders use the presence and breeding status of their neighbors as sources of information to better predict breeding conditions over the duration of the breeding season and to better tailor parental investment to the likelihood of a return on that investment. Exclusive predictions of

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"bird quality" and "information neighborhood" hypotheses can be tested by experimental enhancing or reducing the apparent breeding success of a series of nests, and observing the effects of these manipulations on neighboring, unmanipulated nests.

## INTRODUCTION

Seabirds are classic "k-selected" species that are long-lived and exhibit low levels of annual reproductive output. Ultimately, the reproductive output of seabirds is shaped by a fitness trade-off between adult survival and breeding effort (Pugesek & Diem 1990; Jacobsen et al. 1995; Goulet et al. in press) that may be proximately mediated by adult body condition during the breeding season (Monaghan et al. 1989; Hamer et al. 1993; Chaurand & Weimerskirch 1994; Tveraa et al. 1997; Phillips et al. 1996). Typically food supply is considered the most important proximate constraint on reproductive performance of seabirds (Furness & Birkhead 1984; Monaghan et al. 1989; Harris & Wanless 1990; Hamer et al. 1993; Roberts & Hatch 1993; Phillips et al. 1996) and is believed to affect parental investment through effects on adult body condition. While food supply can explain variability in productivity among years and among colonies, it alone cannot explain spatial heterogeneity (patchiness) in productivity within colonies because seabirds forage many kilometers from breeding sites and, in principle, all individuals should have equal access to a common food resource.

Although individuals within seabird colonies potentially have equal access to food resources, foraging success of individuals may vary for stochastic reasons because prey is patchy and unpredictable in both space and time. If portions of the colony serve as localized information centers (Ward & Zahavi 1973), then differences in foraging success among different information centers could contribute to with-colony variability in productivity. Lastly, individuals nesting in high-density groups might experience enhanced foraging efficiency because, if individual benefit when foraging in groups (Gotmark et al. 1986), nesting groups can serve as "recruitment centers" for foraging groups (Evans 1982).

In contrast, within-colony variability in productivity may be better explained by the localized action of extrinsic physical factors within the colony: localized predation is an often-cited explanation for patchy productivity within seabird colonies (Maunder & Threlfall 1972; Nettleship 1972; Birkhead 1977; Harris 1980); parasites and disease can also cause differences in productivity both among and within breeding colonies (Feare 1976; Duffy 1983); and localized effects of weather may contribute to within-colony variability in chick growth rates (Kildaw 1998) and productivity (Threlfall et al. 1974; Byrd & Tobish 1978; Birkhead & Nettleship 1981).

Patchy productivity may also be a product of differences in quality among individuals (intrinsic differences in parenting abilities due to age, experience, body size), provided that some mechanism promotes localized aggregations of high-quality individuals within breeding colonies. Coulson (1968) documented spatial aggregation of "high quality" individuals (individuals with above-average productivity and survival) at the center of a black-legged kittiwake (Rissa tridactyla) colony in western Britain, and proposed that high-quality individuals become spatially aggregated at the time of recruitment via intense competition for preferred nest sites in the center of the colony.

Social stimulation is another possible source of patchiness in productivity within seabird colonies: Darling (1938) proposed that social stimulation within high density aggregations results in greater reproductive synchrony and enhanced productivity via predator swamping. Although correlations between nest density and synchrony have been observed in some studies (Birkhead 1977; Burger 1979), evidence favoring the social stimulation hypothesis is equivocal (MacRoberts & MacRoberts 1972, Gochfeld 1980).

Over the past 20 years, the reproductive performance of kittiwakes in the North Pacific has been lower and has exhibited greater inter-annual variability than that of kittiwakes in the North Atlantic (Hatch et al. 1993). Although poor and variable productivity of kittiwakes on St. George Island (Dragoo & Dragoo 1996) is potentially a consequence of nest abandonment in response to low food availability, access to food cannot explain prominent patterns of within-colony variability on St. George Island. The

objective of this study was to identify patterns of within-colony variability in the reproductive success of red-legged (R. brevirostris) and black-legged kittiwakes on St. George Island, and to evaluate several hypotheses that potentially explain these patterns.

## METHODS

### Study Area

St. George Island is located in the south-eastern Bering Sea (56° 35' N 169° 35' W) and is the southern-most of the Pribilof Islands. Basalt cliffs that comprise most (40 km) of the island's perimeter support one of the largest assemblages of breeding seabirds in the North Pacific, including estimated breeding populations of 193,900 red-legged and 62,500 black-legged kittiwakes (Kildaw 1998). Kittiwake nests were not uniformly distributed within available habitat, rather they were aggregated into identifiable clusters or subcolonies. Furthermore, although both species nest in equal numbers within low-elevation areas, red-legged kittiwakes nest at extremely high densities within high-elevation areas in the northwestern corner of the island where they outnumber black-legged kittiwakes 22:1 (Kildaw 1998).

### Reproductive Data

We monitored the reproductive performance of red-legged and black-legged kittiwakes on nest-mapping plots that were distributed around the perimeter of St. George Island at locations where nests could be viewed from a nearby (< 200 m), cliff-top vantage point. Plots were not randomly selected: most were located within 100 m of the cliff top and were concentrated in areas where the cliff edge was more convoluted. We monitored kittiwake reproduction on a total of 211 nest-mapping plots in each summer of 1993 - 1995 and on 132 additional plots in 1994 and 1995. In each year we visited mapping plots during early-laying (early June) and mid-incubation periods (early July) and marked the locations of nest attempts (sites with a level disk of nest material estimated to be > 15 cm in diameter and > 5 cm thick at the seaward edge) directly onto

laminated, 5" x 7" photographs of each plot using a permanent marker. We determined the reproductive fate of marked nests just prior to the initiation of fledging, classifying nests that were either empty or no longer present as "failed" and nests that contained large chicks with visible tail feathers or complete contour feather coverage on their backs and wings as "successful" (18 - 20 days old, pers. obs.). Although the minimum fledging age of kittiwake chicks is approximately 30 - 35 days (Maunder & Threlfall 1972), little mortality occurs after 20 days in either species (pers. obs.); thus, survival to 20 days is a good proxy for survival to fledging. If, during the initial pre-fledging visit, one or more nests on a plot could not be classified as either successful or failed (because they contained young chicks or nest contents were obscured by adults), we re-visited the plot every 10 - 14 days until the fate of all nests was determined. In the few instances where nest fate could not be determined prior to the end of the field season, we classified nests containing chicks on the last visit as "successful" and all others as "failed". For each species on each plot we tallied the number of successful and failed nests and determined productivity (successful nests / nest attempts).

In addition, we estimated the elevation of each plot from a detailed topographic map of St. George Island, categorizing the elevation of each plot as either low (0 - 100 m), medium (>100 m - 200 m), or high (> 200 m). We categorized the general aspect of the cliff within 1 km of each plot as either north (N, NE, NW) or other (all other directions) and assigned an ordinal nest density score (low, medium, high) to each plot based on the number and spatial distribution of nests: high-density plots contained > 15 nests, of which > 50% were either centrally located (vs. peripherally located, where the external angle formed by a line connecting any three adjacent peripheral nests > 90°), or were located within 2 kittiwake body lengths of ≥ 3 other nests. Medium-density plots contained ≥ 10 nests, of which 20% - 50% were either centrally located or were located within 2 kittiwake body lengths of ≥ 3 other nests. All remaining plots were categorized as "low-density". We determined species composition of each plot (red-legged kittiwake nests/total nests), and categorized the number of nests of each species as one of the

following size classes: 1 - 9 nests, 10 - 19 nests, 20 - 40 nests, and > 40 nests.

Assessing Variability among Plots

We compared kittiwake productivity among plots by performing a G (log-likelihood ratio) test of independence for each species, within each year, and restricted these analyses to plots with > 5 nests to ensure that average expected counts exceeded 6 nests per cell (Zar 1996). Because of nearly complete reproductive failure of black-legged kittiwakes in 1995 (only 7 of 1007 nests on study plots fledged chicks), we excluded data for black-legged kittiwakes in 1995 from this and all subsequent analyses. For each species in each year, we graphically compared the observed distribution of plot productivities to that expected from a random distribution which was generated (via 1000 iterations) by calculating the overall productivity of a given species in a given year and assuming that the reproductive fates of nests were independent of one another.

We then performed a series of univariate analyses for each species within each year to determine effects of physical factors (plot elevation and aspect) and social factors (nest density and species composition) on kittiwake productivity (Mann-Whitney U tests for factors with two levels, Kruskal-Wallis tests for factors with > 2 levels). Univariate analyses were not conclusive because they were confounded by inter-correlations between factors which all differed markedly between the high- and low-elevation areas of St. George Island. Although we could not perform the appropriate 4-factor analysis required to disentangle the effects of these inter-related factors (because all combinations of factors do not exist on St. George Island), we were able to evaluate the effects of nest density and plot elevation on the productivity of each species by restricting the analysis to a sample of plots that shared attributes of the other two factors: for red-legged kittiwakes we performed a two-factor ANOVA on rank-transformed productivity data using a subset of plots that were all north-facing, and were > 50 % red-legged kittiwake in species composition. We merged low and medium elevation categories in this analysis because of small sample sizes at low elevations. For black-legged kittiwakes, we performed a similar

analysis on data from north-facing plots but merged medium and high elevation categories to compensate for small sample sizes at high elevation. In addition, we included all plots regardless of species composition in this analysis because we lacked sufficient data to otherwise restrict the analysis. I also restricted analyses to plots with data in all three years for red-legged kittiwakes and in both 1993 and 1994 for black-legged kittiwakes. Furthermore, to reduce the unwarranted influence of plots with very few nests (hence productivity is highly variable due to binomial "noise") or very many nests, we weighted plots with fewer than 10 nests by a factor of "# nests / 10".

To determine whether effects of elevation, aspect, nest density, plot size, and species composition accounted for within-colony variability in kittiwake productivity, we performed G tests on samples of plots that shared all of these characteristics in common. We limited these analyses to red-legged kittiwakes only (we lacked sufficient data for analyses of black-legged kittiwakes) and restricted samples to north-facing plots that were > 50% red-legged kittiwake in species composition. We pooled samples from adjacent size categories where the number of plots within a given elevation x density x size category did not exceed 5, and excluded plots with fewer than 10 nests to ensure that mean expected cell counts in these analyses were > 6 (Zar 1996). Finally, we did not perform analyses for samples in which the mean expected frequency of either *successful* or failed nests across plots was < 1.

Assessing Plot and Nest-Site Consistency among Years

We assessed plot consistency across years using samples of plots that were observed in each year of the study, were located on north-facing cliffs, were > 50 % red-legged kittiwake in species composition, and that shared characteristics of elevation, nest density, and plot size. For red-legged kittiwakes, we evaluated among-year consistency in rankings of productivity among plots for these samples using Kendall's coefficient of concordance (Zar 1996), but did not perform analyses for black-legged kittiwakes because of insufficient data.

We evaluated among-year consistency in the productivity of individual red-legged kittiwake nest sites using data from 9 high-, 13 medium-, and 10 low-density plots that were all located at high-elevation, were north-facing, and were > 50 % red-legged kittiwake in species composition. We did not perform similar analyses for black-legged kittiwakes, or for red-legged kittiwakes at low elevation. Kittiwakes on St. George Island exhibit high annual survival (Dragoo & Dragoo 1996) and fidelity to mates and nest sites between years. For example, banded red-legged kittiwakes within one high-density plot at high-elevation exhibited 83% inter-annual nest-site fidelity over the three years of this study (D. Kildaw, unpublished data). Although high fidelity appears to be the general rule for kittiwakes (ref), mass relocations of banded kittiwakes were observed within one low-elevation area on St. George Island between 1995 and 1996 breeding seasons (D. Kildaw, unpublished data), and suggested that fidelity may be variable and localized. In these analyses, we assumed that consistency in nest-site productivity across years reflects consistency of breeding pairs occupying those sites.

We evaluated nest-site consistency across all three years of the study (1993-1995) by performing goodness-of-fit, G tests on data pooled from all plots within each density category. Prior to pooling, we tallied the number of nests within each plot that exhibited extreme productivity (either succeeded or failed in all 3 years) and the number that exhibited mixed reproductive fates across years. We computed expected values for G tests using the overall productivity (# successful nests / total nest attempts) of each plot in each year and assuming that nest fate in one year was independent of nest fate in other years (the null hypothesis). Within each nest density category, we then pooled both observed and expected counts across plots for both extreme, and mixed-fate nest categories, and performed a G test on the resulting totals. If nest sites exhibit consistent productivity across years, then the "extreme" category will be significantly over-represented in the sample.

Predator Observations

To evaluate the contribution of patchy predation to within-colony variability in reproductive performance, we conducted opportunistic observations of the activities of predators in the vicinity of bird breeding cliffs during the summers of 1993-95. Potential predators of kittiwake eggs, nestlings, and adults on St. George Island include arctic foxes (Alopex lagopus), larid gulls (primarily non-breeding glaucous-winged gulls, Larus glaucescens), and several common ravens (Corvus corax). We also monitored the reproductive fate of approximately 500 kittiwake nests accessed by rope or ladder every 3 - 5 days and documented any evidence of predation on eggs or chicks.

Parasites

For 5 plots at high elevation, and 16 plots at low elevation, we used palpation to document the presence or absence of ticks (Ixodes spp.) on nestling kittiwakes during periodic weighings conducted every 3 -5 days from hatching to an age of 35 days. For each plot in each year we determined the number of red-legged and black-legged kittiwake chicks that survived > 7 days (to exclude newly hatched chicks with limited exposure to ticks) and determined the proportion of chicks of each species that were infested with ticks at any time during development. We compared tick infestation (# infested chicks / total chicks) between the two species with a Wilcoxon paired-sample test, pairing within each plot and pooling data from all years. Following these preliminary analyses, we pooled data from the two species (infestation did not differ between species) and compared infestation between elevations and among years with a two-factor ANOVA performed on rank-transformed data.

## RESULTS

Variability among Plots

G tests indicated that productivity differed significantly among plots for red-legged kittiwakes in all three years (all $P < 0.001$) and for black-legged kittiwakes in

1993 and 1994 (we disregarded data for black-legged kittiwakes in 1995 in this and all subsequent analyses because of nearly total reproductive failure). For both species in all years, nests within plots shared a common reproductive fate to a greater extent than was expected by chance (binomial variation), and plot productivities were over-distributed relative to expected distributions (e.g., Fig. 4.1).

To determine the origin of among-plot variability, we performed univariate analyses on each species in each year for five factors that potentially influence kittiwake reproductive success. We found that productivity was significantly greater ($\underline{P} > 0.05$) for high-density (5/5 tests), high-elevation (3/5 tests), plots that were > 50 % red-legged kittiwake in species composition (2/5 tests), and were north-facing (1/5 tests). Unfortunately, these 5 factors differed markedly and jointly between plots at high-elevation and low-elevation areas of the island; hereafter, we refer to the joint affect of these factors as the "High Bluff" effect.

We evaluated the contribution of nest density and plot elevation to the "High Bluff" effect by performing a two-factor ANOVA for each species in each year using north-facing plots that were > 50 % red-legged kittiwake in species composition. For red-legged kittiwakes we found significant effects of density in all three years (1993: $\underline{F}_{2,135} = 9.1$, $\underline{P} = 0.0002$, 1994: $\underline{F}_{2,135} = 10.7$, $\underline{P} = 0.0001$, 1995: $\underline{F}_{2,135} = 5.8$, $\underline{P} = 0.004$), significant effects of elevation in 1994 ($\underline{F}_{1,135} = 25.5$, $\underline{P} = 0.0001$) and 1995 ($\underline{F}_{1,135} = 9.1$, $\underline{P} = 0.003$), but no density x elevation interaction in any year (Fig. 4.2). For black-legged kittiwakes we found significant effects of only nest density in both 1993 ($\underline{F}_{2,79} = 4.8$, $\underline{P} = 0.011$) and 1994 ($\underline{F}_{2,79} = 11.7$, $\underline{P} = 0.0001$), the only years tested (Fig. 4.3). Visual inspection of Figs. 4.2 and 4.3 suggests that, for both species, productivity was greater on high-density plots and, for red-legged kittiwakes, productivity was greater at high elevation in 1994 and 1995.

To determine whether the "High Bluff" effect explained within-colony variability in kittiwake productivity on St. George Island, we controlled for the High Bluff effect by performing $\underline{G}$ tests on sub-samples of plots that shared physical and social characteristics

in common. These "within area" analyses were restricted to red-legged kittiwakes only. Of 13 G-tests performed on samples of high-elevation plots, 11 indicated significant variability in productivity among plots ($P < 0.05$). Of 9 such analyses for plots within the two lower-elevation categories, 8 revealed significant variability among plots ($P < 0.05$). Thus, the High Bluff effect does not account for all among-plot variability because significant variability exists even among plots that share all characteristics of aspect, elevation, nest density, plot size, and species composition (e.g., Fig. 4.4). Hereafter we refer to variability among plots with similar characteristics as the "Within Area" effect.

Plot and Nest-Site Consistency among Years

We evaluated plot consistency across the three years of the study using Kendall's concordance analysis and found consistency ($P < 0.05$) among high-elevation, high-density plots (2 of 2 tests) but a lack of consistency ($P > 0.05$) among plots for all other combinations of density and elevation tested (9 of 9 tests); however, in all tests lacking statistical significance, there was a trend toward consistency among years, and for three of these analyses $P < 0.10$.

We performed G-tests on the fate of individual nest sites among years and determined that the reproductive fate of breeding pairs was more consistent than expected by chance within high-density plots ($n = 422$, $G_1 = 12.5$, $P < 0.001$), but not within medium ($n = 246$, $G_1 = 3.2$, $P > 0.05$), or low-density plots ($n = 68$, $G_1 = 0.64$, $P > 0.05$).

Predator Observations

Predators are not an important source of nest failure for kittiwakes breeding on St. George Island. Larid gulls are abundant along the coastal cliffs of St. George; however, they did not harass nesting kittiwakes and did not remove kittiwake eggs even from unattended nest sites. We observed several instances where abandoned kittiwake eggs remained at the nest site for more than a month before eventually disappearing. Furthermore, although arctic foxes do obtain some kittiwake eggs early in the season

(pers. obs.), foxes cannot access most kittiwake nests sites and target murre eggs (murre eggs are more numerous, and 2-3x the volume of a kittiwake egg) as soon as murres begin laying (pers. obs.).

Parasites

Tick infestation did not differ between red-legged and black-legged kittiwakes (Sign rank = 0, $n = 9$, $P = 1.0$); therefore, we pooled species within each plot prior to subsequent analyses. A two-factor ANOVA performed on rank-transformed data indicated that tick infestation differed among years ($F_{2,39}$ df = 25.1, $P < 0.001$) and was significantly greater for plots at low vs. high elevation ($F_{1,39}$ df = 10.5, $P = 0.002$). In addition, the year x elevation interaction was significant ($F_{2,39}$ df = 4.8, $P = 0.01$), indicating that the relationship between tick infestation and year differed between high and low elevation areas. In 1993, infestation was negligible within both low- and high-elevation areas, but in 1994 and 1995 infestation was greater within low-elevation plots (Fig. 4.5).

## DISCUSSION

We found significantly greater spatial heterogeneity (patchiness) in kittiwake reproductive performance than could be explained by the null expectation of a random and independent distribution of reproductive fate among nest sites. Nests within plots shared a common reproductive fate to a greater degree than was expected by chance. Univariate analyses suggested that several factors (aspect, elevation, nest density, and species composition) potentially influence the productivity of both kittiwake species and further analyses, which controlled for elevation and species composition, revealed that kittiwake productivity was positively related to both density of nests and elevation.

We identified two prominent patterns of within-island variability in kittiwake productivity: 1) the "High Bluff" effect - regional differences in productivity within the island, and 2) the "Within Area" effect - variability among plots with similar physical and

social characteristics. Although the High Bluff effect was apparent in both species, we restrict our discussion to red-legged kittiwakes because data for black-legged kittiwakes were insufficient to evaluate Within Area effects or to perform additional analyses necessary to evaluate the several hypotheses for within-colony variability that we address below.

Predation

Although localized predation is a potential source of reproductive variability, it cannot explain patterns of productivity observed in this study because predation was not a significant source of nest failure for kittiwakes on St. George Island during this study. Indeed, the absence of aerial predators on St. George Island presents a rare opportunity to study the action of other factors in the absence of the confounding effects of predation. When predators are abundant it is difficult to distinguish true predation events from instances of opportunistic predation on abandoned eggs and chicks.

Weather

Localized weather conditions are not responsible for the High Bluff effect because differences in reproductive performance between high- and low-elevation areas are contrary to patterns predicted by the weather hypothesis: kittiwakes exhibited enhanced reproductive performance at high, vs. low elevations despite being exposed to generally colder (an elevation effect), wetter (due to persistent fog), and windier conditions (pers. obs.). Furthermore, weather does not explain Within Area variability in kittiwake productivity because productivity varied among plots even though they shared characteristics of both elevation and aspect, and hence experienced similar weather conditions.

Parasites

Hard ticks (Ixodes spp.) are widespread and abundant hematophagous ecto-

parasites of seabirds that may affect seabird reproduction directly though blood loss or indirectly by transmitting parasites and disease (Feare 1976; Nuttall 1984). Ixodes uriae, a generalist seabird tick, requires three separate blood meals and 4 or more years to complete its life cycle (Eveleigh & Threlfall 1974). Because ticks are only attached to their hosts for the 5 - 7 days necessary to obtain each blood meal, overlapping generations of ticks spend most of their lives associated with nesting substrate within seabird colonies (Eveleigh & Threlfall 1974).

Kittiwake productivity was negatively related to tick infestation both between elevations and across years. Thus, tick infestation potentially explains differences in reproductive performance between high and low elevation areas (the High Bluff effect). Productivity of both kittiwake species did not differ between elevation categories in 1993, a year of low tick abundance in both low, and high-elevation areas; however, productivity declined overall in both 1994 and 1995, years in which tick infestation was greater overall, and was particularly suppressed at low elevation (Figs. 4.2 + 4.3) were infestation was particularly severe (Fig. 4.5). In contrast, ticks are not responsible for the Within Area effect because productivity varied significantly among plots in 1993, despite negligible levels of tick infestation throughout the study area.

As a cautionary note, the correlations between productivity and tick infestation do not necessarily imply causation. Although ticks potentially influence kittiwake productivity, high rates of tick infestation may be a consequence, rather than a cause, of low reproductive success. In years of poor productivity, ticks might become concentrated on the few available nestlings within each plot. Furthermore, the observed pattern of greater parasite infestation at low-density, low-elevation areas of St. George Island runs counter the pattern of positive density dependance predicted by theory and observed for other species of seabirds (Eveleigh & Threlfall 1974). One possible explanation for this contradiction is that colder, windier weather conditions at High Bluff are less conducive to overwinter survival of ticks.

Enhanced Foraging Efficiency

The information center hypothesis proposes that individuals in colonies may benefit by exploiting information provided by other foragers (either intentionally or unintentionally) on the location of high quality foraging areas (Ward & Zahavi 1973). If plots serve as localized information centers, then Within Area variability in kittiwake productivity could result from differences in the effectiveness of local information centers and the High Bluff effect could be a consequence of better information within high-density plots. On the other hand, although seabirds may exchange information within foraging areas through "network foraging" (Wittenberger & Hunt 1985) and may orient towards returning foragers when loafing or en route to foraging areas (Burger 1997), evidence that seabirds colonies potentially serve as localized information centers is equivocal (e.g., Waltz 1987, vs. Gotmark 1990), and is limited to species that have short transit times to foraging areas relative to the persistence of resource patches (Greene 1987; Waltz 1987). In contrast, kittiwakes on St. George Island typically forage 40 - 100+ km from the colony (Schneider & Hunt 1984) on ephemeral prey patches that do not persist long enough for departing individuals to benefit from information from returning foragers. Indeed, recent observations of the foraging patterns of black-legged kittiwakes suggest that individuals do not exploit information centers; rather, they use habitual foraging areas which differ among colony members and even between individuals of mated pairs (Irons 1998).

Alternately, effects of density on kittiwake productivity may arise because individuals benefit by foraging in groups and breeding colonies serve as "recruitment centers" (Evans 1982) for foraging groups. Although flock-foraging advantages have been documented for kittiwakes (Bayer 1983) and other larids (Gotmark et al. 1986), foraging groups can form spontaneously within foraging areas without the benefit of the recruitment centers. Furthermore, there is no evidence that recruitment of foraging groups at the breeding colony is restricted within localized clusters of individuals.

Bird Quality Hypothesis

Within-island variability in kittiwake productivity is potentially a consequence of spatial segregation of individuals that differ intrinsically in foraging or parenting abilities. Coulson (1968) proposed that intense competition among black-legged kittiwakes for preferred nest sites at the colony center promoted spatial segregation of individuals that differed intrinsically in both reproductive performance and probability of survival. On St. George Island, kittiwakes prefer nest sites located within high-density plots of conspecifics (Kildaw, in press); therefore, consistently greater productivity of kittiwakes in high vs. low-density plots (the High Bluff effect) might be a consequence of the aggregation of high-quality individuals within high-density plots via Coulson's mechanism. In contrast, the bird-quality hypothesis cannot explain high productivity of black-legged kittiwakes within high-elevation plots because it predicts the highest-quality black-legged kittiwakes should recruit into low-elevation plots that are numerically dominated by black-legged kittiwakes.

Furthermore, the bird quality hypothesis potentially explains Within Area variability in kittiwake productivity because bird quality may differ among plots despite similarities in physical and social characteristics. We evaluated two predictions of the bird quality hypothesis, that plot and individual nest sites should exhibit inter-annual reproductive consistency, but found plot and nest-site consistency only among high-density plots located at high elevations. These analyses assume that nest-site fidelity of kittiwakes is uniformly high across all categories of nest density and elevation. On the other hand, although kittiwakes generally exhibit high fidelity on St. George Island (D. Kildaw, unpublished data) and elsewhere (Coulson & Thomas 1983), widespread relocations of banded kittiwakes observed within a low-elevation area on St. George Island between 1995 and 1996 breeding seasons, potentially explain the lack of breeding consistency observed in lower-density and lower-elevation plots.

Regardless, patchy bird quality potentially explains some within-colony patterns of kittiwake productivity; however, its proposed proximate mechanism (the preference of

kittiwakes for high density aggregations of conspecifics) requires an ultimate explanation. High density groups may attract higher quality recruits because, in addition to anti-predator advantages of grouping (Birkhead 1977; Anderson & Hodum 1993), recent studies suggest that prospecting kittiwakes may also use the presence and reproductive performance of established breeders as indicators of local habitat quality (Forbes & Kaiser 1994; Boulinier et al. 1996).

Social Information and the "Information Neighborhood"

Spatial clustering of successful and failed nests within plots and enhanced productivity of high-density groups suggest that breeding kittiwakes may be influenced by the presence of neighbors; however, the "social stimulation" hypothesis originally proposed by Darling (1938) is not tenable because its proposed mechanism and ultimate explanation (predator swamping via breeding synchrony) is not applicable on St. George Island (predation is not an important source of nest failure). Therefore, we propose a new concept, the "information neighborhood" hypothesis, to explain spatial clustering of successful and failed nests and Within Area effects on St. George Island that can function in the absence of "selfish herd" benefits or "information centers".

Recent research has shown that information provided by the presence and reproductive success of breeding seabirds is a valuable commodity that shapes nest-site selection of prospecting seabirds and demographic trends within breeding colonies (Forbes & Kaiser 1994; Boulinier et al. 1996; Danchin & Wagner 1997). The "information neighborhood" hypothesis is a related concept which proposes that colonial breeders use the presence and breeding status of their neighbors as a source of information to better predict breeding conditions over the duration of the breeding season and to better tailor parental investment to the likelihood of return on that investment. An inherent assumption of this hypothesis is that breeders are faced with a fitness tradeoff between current and future fecundity; otherwise there can be no cost of reproduction and, by definition, no parental investment. Survival and fecundity costs of reproduction have

been documented experimentally for kittiwakes (Jacobsen et al. 1995: Goulet et al. in press) and for other seabirds (Wernham & Bryant 1998).

Foraging success of individuals is highly variable because prey of pelagic seabirds is patchy and unpredictable in both time and space. As a consequence, the average foraging success of a group of individuals is likely a better predictor of future conditions than is the foraging success of a single individual. Thus, breeders that use the reproductive status of neighbors as a surrogate measure of their foraging experiences, can more accurately assess general, and thus, future foraging conditions. Furthermore, although the information neighborhood hypothesis can function in a predator vacuum, where predators are an important source of reproductive failure and the breeding status of neighbors influences predation risk (Birkhead 1977; Anderson & Hodum 1993; Murphy & Schauer 1996), breeders can also use the "information neighborhood" to better predict predation risk over the course of the breeding season and better tailor parental investment to the likelihood of return on that investment.

Individuals in good body condition experience little cost of reproduction (little fitness tradeoff between current and future reproduction) and should not be influenced by their neighbors. Likewise, individuals in poor body condition faced with extreme costs of reproduction should curtail parental investment regardless of the reproductive status of their neighbors. In contrast, individuals in marginal body condition should exploit the information neighborhood because in doing so they can better match their level of parental investment to their likelihood of successful reproduction. Where neighbors are doing poorly reproductively, individuals in marginal body condition should curtail parental investment because prospects for a fitness return on that investment are poor. On the other hand, where neighbors are doing well reproductively, individuals in marginal body condition should continue providing parental investment because prospects are better for a fitness return on that investment. For example an individual that has by chance encountered poor foraging conditions in the past several weeks should persists with breeding if most of is neighbors encountered good foraging conditions over that

same time period because they suggest that future foraging conditions will be better than that indicated by its own foraging experiences.

The "information neighborhood" can only explain patchy productivity if neighborhoods are localized within breeding colonies. Ideally, breeders should make use of information from as many other colony mates as possible. However, constraints on acquisition of information may limit the effective scope of the "information neighborhood" to nearby individuals only. Although breeders can obtain productivity (proportion of nests which are active) information from hundreds of nests with little cost of assessment, productivity is a crude measure that integrates cumulative breeding conditions over a long window of time. On the other hand, cliff nesting seabirds spend long periods incubating and brooding at the nest site, and potentially can obtain more detailed and current information on breeding conditions from immediate neighbors. For example, breeders could monitor feeding rates of chicks, patterns of mate exchange, patterns of nest attendance (in particular, periods of temporary nest abandonment that might reflect energetic stress), and local prevalence and success of predators. Relative to productivity information, local information is current, more detailed, and more reliable as a predictor of future breeding conditions.

## Conclusions

In this study we document patchiness in productivity of a cliff-nesting seabird at a spatial scale rarely addressed by seabird ecologists. Moreover, these patterns cannot be explained by localized effects of predators, foraging conditions, or weather, three factors traditionally invoked to explain reproductive variability within colonies, among colonies, and among years. Furthermore, parasites, which can influence productivity (Feare 1976; Duffy 1983) and demographic patterns within seabird colonies (Danchin & Monnat 1992; Boulinier & Danchin 1996), can only partially account for these patterns. In the absence of predation, we propose that bird quality may explain enhanced productivity of kittiwakes in high-density groups and that Within Area variability may be a product of

bird quality or localized "information neighborhoods".

Although our results are consistent with the "information neighborhood" hypothesis, our observational data cannot be used to rigorously test this hypothesis. On the other hand, the "information neighborhood" hypothesis generates experimentally testable predictions that are distinct from bird quality, social facilitation, and information center hypotheses. For example, reproductive performance of "experimental" nests can be manipulated via removal of eggs or food supplementation (e.g. Wernham & Bryant 1998), and the response of neighboring, unmanipulated "focal" nests could be monitored. In the absence of predators, the information neighborhood hypothesis exclusively predicts treatment effects on the parental investment of "focal" adults that should be manifest as differences in productivity and/or chick growth rates.

Beyond its potential to explain reproductive variability among subcolonies and the clustering of successful and failed nest sites within subcolonies, the information neighborhood hypothesis has implications for our general understanding of the evolution of coloniality in species dependent on unpredictable food resources. A universal advantage of coloniality may be the potential for information exchange among individuals which can be employed to make adaptive decisions (e.g. Danchin & Wagner 1997).

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## REFERENCES

Anderson, D. J., & Hodum, P. J. 1993. Predator behavior favors clumped nesting in an oceanic seabird. Ecology,74, 2462-2464.

Bayer, R. D. 1983. Black-legged kittiwake feeding flocks in Alaska: selfish/reciprocal altruistic flocks? J. Field Ornithol., 54, 196-199.

Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the common guillemot Uria aalge. J. of Anim. Ecol., 46, 751-764.

Birkhead, T. R., & Nettleship, D. N. 1981. Reproductive biology of thick-billed murres (Uria lomvia): an inter-colony comparison. Auk, 98, 258-269.

Boulinier, T., & Danchin, E. 1996. Population trends in kittiwake colonies in relation to tick infestation. Ibis,138, 326-334.

Boulinier, T., Danchin, E., Monnat, J., Droutrelant, C., & Cadiou, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. J. of Avian Biol., 27, 252-256.

Burger, J. 1979. Colony size: a test for breeding synchrony in herring gull (Larus argentatus) colonies. Auk, 96, 649-703.

Burger, A. E. 1997. Arrival and departure behavior of Common Murres at colonies: Evidence for an information halo? Colonial Waterbirds, 20, 55-65.

Byrd, G. V., & T. G. Tobish. 1978. Wind-caused mortality in a kittiwake colony at Buldir Island, Alaska. Murrelet, 59, 37.

Chaurand, T., & Weimerskirch, H. 1994. Incubation routine, body mass regulation and egg neglect in the blue petrel Halobaiena caerulea. Ibis, 136, 285-290.

Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the

edges of a colony. Nature, 217, 478-479.

Coulson, J. C., & Thomas, C. S. 1983. Mate choice in the kittiwake gull. In: Mate Choice. (Ed. by P. P. G. Bateson), pp. 141-164. Cambridge UK: Cambridge University Press.

Danchin, E., & Monnat, J. Y. 1992. Population dynamics modeling of two neighbouring kittiwake Rissa tridactyla colonies. Ardea, 80, 171-180.

Danchin, E., & Wagner, R. H. 1997. The evolution of coloniality: the emergence of new perspectives. Tree, 12, 342-347.

Darling, F. F. 1938. Bird flocks and the breeding cycle. A contribution to the study of avian sociality. Cambridge, U.K: Cambridge University Press.

Dragoo, D. E., & Dragoo, B. K. 1996. Results of productivity monitoring of kittiwakes and murres at St. George Island, Alaska, in 1995. Homer, Alaska, USA: United States Fish and Wildlife Service.

Duffy, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. Ecology, 64, 110-119.

Evans, R. M. 1982. Foraging flock recruitment at a black-billed gull colony: implications for the information center hypothesis. Auk, 99, 24-30.

Eveleigh, E. S., & Threlfall, W. 1974. The biology of Ixodes (Ceratixodes) uriae White, 1852 in Newfoundland. Acarologia, 16, 621-635.

Feare, C. J. 1976. Desertion and abnormal development in a colony of sooty terns infested with virus-infected ticks. Ibis, 18, 112-115.

Forbes, L. S., & Kaiser, G. W. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. Oikos, 79, 377-384.

Furness, R W. & Birkhead, T. R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature, 311, 655-656.

Galbraith, H. 1983. The diet and feeding ecology of breeding kittiwakes Rissa tridactyla. Bird Study, 30, 109-120.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in

colonial seabirds. In: Behavior of marine animals. (Ed. by J. Burger, B. L. Olla, and H. E. Winn), pp. 207-270. New York USA: Plenum Press.

Gotmark, F., Winkler, D. W., & Andersson, M. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature, 319, 589-591.

Gotmark, F. 1990. A test of the information-center hypothesis in a colony of sandwich terns Sterna sandvicensis. Anim. Behav., 39, 487-495.

Greene, E. 1987. Individuals in an osprey colony discriminate between high and low quality information. Nature, 329, 239-241.

Goulet, G. H., Irons, D. B., & Estes J. A. In press. Survival cost of chick rearing in black-legged kittiwakes. J. Anim. Ecol.

Hamer, K. C., Monaghan, P., Uttley, J. D., Walton, P., & Burns, M. D. 1993. The influence of food supply on the breeding ecology of kittiwakes Rissa tridactyla in Shetland. Ibis, 135, 255-263.

Harris, M. P. 1980. Breeding performance of puffins Fratercula arctica in relation to nest density, laying date and year. Ibis, 122, 193-209.

Harris, M. P. & Wanless, S. 1990. Breeding success of British kittiwakes Rissa tridactyla in 1986-88: evidence for changing conditions in the northern north sea. J. Appl. Ecol., 27, 172-187.

Hatch, S. A., Byrd, G. V., Irons, D. B., & Hunt, G. L. 1993. Status and ecology of kittiwakes (Rissa tridactyla and R. brevirostris) in the North Pacific. In: The status, ecology, and conservation of marine birds in the north Pacific. (Ed. by K. T. Briggs, K. H. Morgan, and D. Seigel-Causey), pp. 140-153. Ottawa, Canada: Canadian Wildlife Service Special Publication.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology, 79, 647-655.

Jacobsen, K. O., Erikstad, K. E, & Saether, B. E. 1995. An experimental study of the costs of reproduction in the kittiwake Rissa tridactyla. Ecology, 75, 1636-1642.

Kildaw, S. D. 1998. Population status and patterns of distribution and productivity of

kittiwakes on St. George Island, Alaska. Ph. D. thesis. University of Alaska Fairbanks, Fairbanks Alaska, USA.

Kildaw, S. D. In press. Competitive displacement? An experimental assessment of nest-site preferences of cliff-nesting gulls. Ecology.

MacRoberts, B. R., & MacRoberts, M. H. 1972. Social stimulation of reproduction in herring and lesser black-backed gulls. Ibis, 114, 495-506.

Maunder J. E., & W. Threlfall. 1972. The breeding biology of the black-legged kittiwake in Newfoundland. Auk, 89, 789-816.

Monaghan, P., Uttley, J. D., Burns, M. D., Thaine C., & Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in arctic terns Sterna paradisaea. J. Anim. Ecol., 58, 261-274.

Murphy, E. C., & Schauer, J. H. 1996. Synchrony in egg-laying and reproductive success of neighboring common murres, Uria aalge. Behav. Ecol. Sociobiol., 39, 245-258.

Nettleship, D. N. 1972. Breeding success of the common puffin (Fratercula arctica (L.)) on different habitats at Great Island, Newfoundland. Ecol.Mono., 42, 239-268.

Nuttall, P. A. 1984. Tick-borne viruses in seabird colonies. Seabird, 7, 31-41.

Phillips R. A., Caldow, W. G., & Furness, R. W. 1996. The influence of food availability on the breeding effort and reproductive success of arctic skuas Stercorius parasiticus. Ibis, 138, 410-419.

Pugesek, B. H., &. Diem, K. L. 1990. The relationship between reproduction and survival in known-aged California gulls. Ecology, 71, 811-817.

Roberts, B. D., & Hatch, S. A. 1993. Behavioral ecology of black-legged kittiwakes during chick rearing in a failing colony. Condor, 95, 330-342.

Schneider, D., & Hunt, G. L., Jr. 1984. A comparison of seabird diets and foraging distributions around the Pribilof Islands, Alaska. In: Marine birds: their feeding ecology and commercial fisheries relationships. (Ed. by D. N. Nettleship, G. A. Sanger & P.F. Springer), pp. 86-95. Ottawa, Canada: Canadian Wildlife Service

Occasional Publication.

Threlfall, W., Eveleigh, E., & Maunder, J. E. 1974. Seabird mortality in a storm. Auk, 91, 846-849.

Tveraa, T., Lorentsen, S., & Saether, B. 1997. Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (Thalassoica antarctica). Behav. Ecol., 8, 465-469.

Waltz, E. C. 1987. A test of the information-centre hypothesis in two colonies of common terns, Sterna hirundo. Anim. Behav., 35, 48-59.

Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as "information centers" for food-finding. Ibis, 115, 517-534.

Wernham, C. V., & Bryant, D. M. 1998. An experimental study of reduced parental effort and future reproductive success in the puffin, Fratercula arctica. J. Anim Ecol., 67, 25-40.

Wittenberger, J. F., &. Hunt, G. L., Jr. 1985. The adaptive significance of coloniality in birds. In: Avian Biology VIII (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 1-78. New York, New York, USA: Academic Press.

Zar, J. H. 1996. Biostatistical analysis. 3rd edition. Englewood Cliffs, New Jersey, USA: Prentice-Hall.

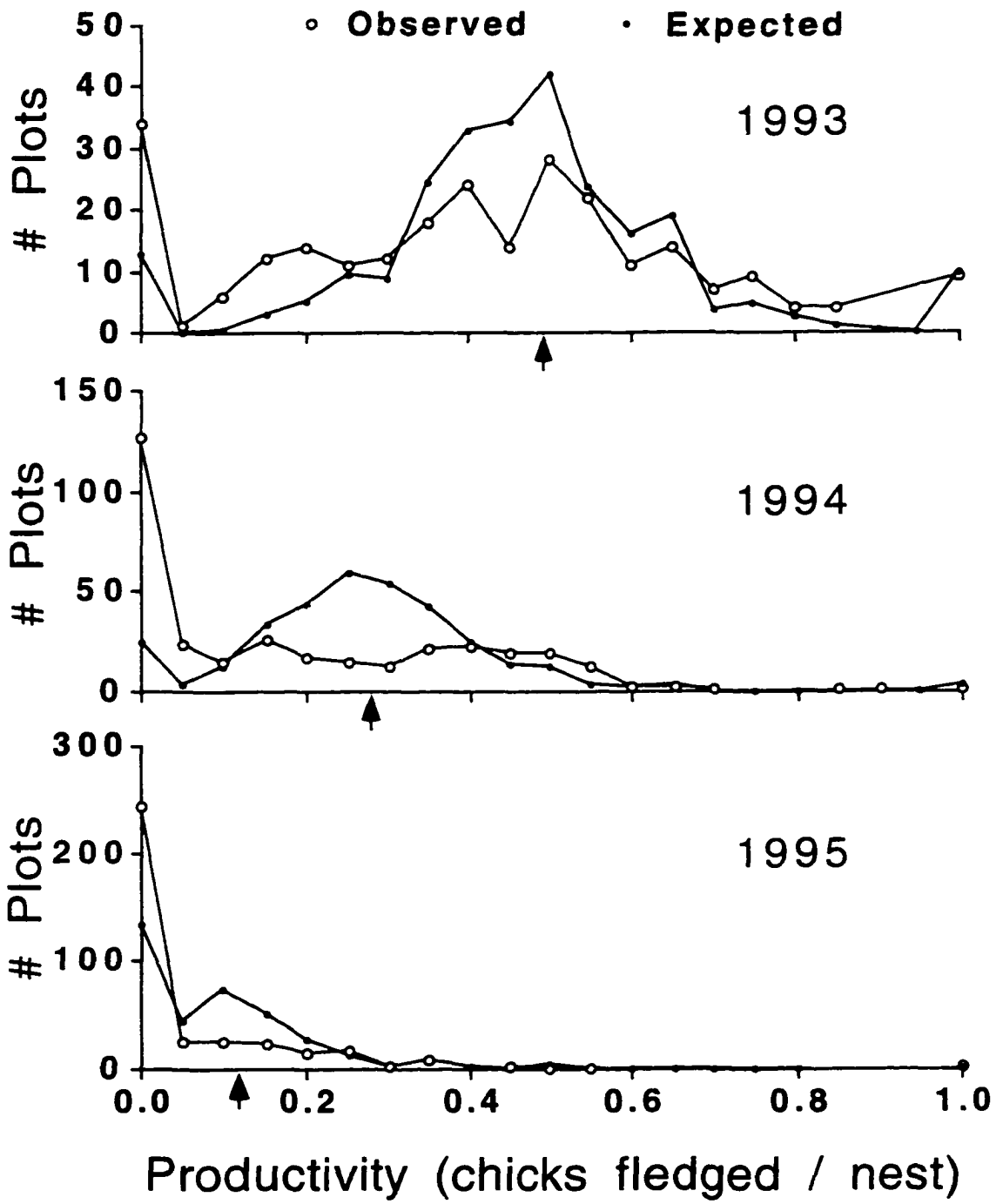



Figure 4.1. Observed and expected distributions of kittiwake productivity. Data for red-legged kittiwakes in 1993, 1994, and 1995 are presented. Expected values are over-distributed relative to expected distributions. Arrows denote annual mean productivity.

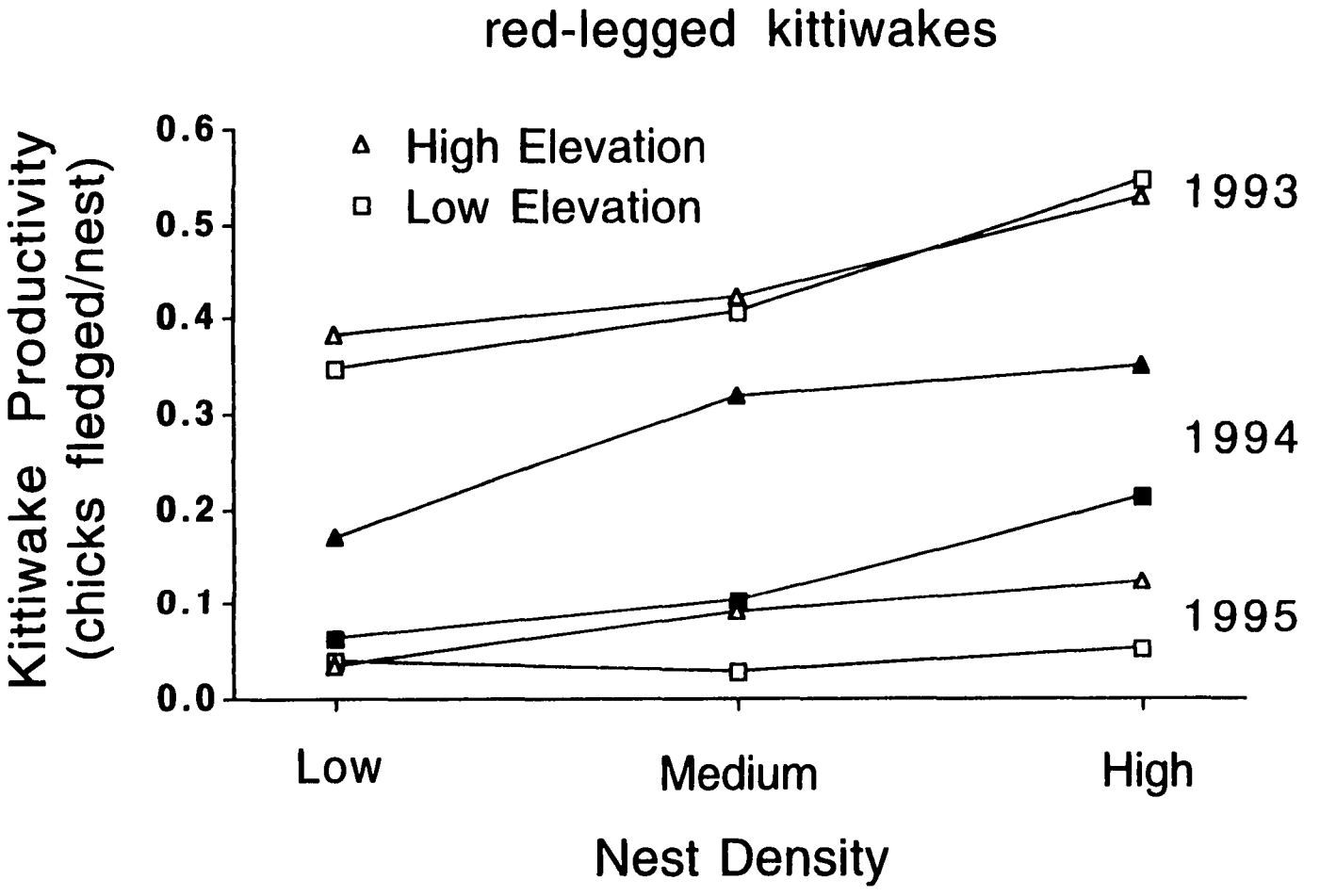



Figure 4.2. Within-island patterns of red-legged kittiwake productivity. Productivity was greater on high-density plots in all years, and was greater on high-elevation plots in 1994 and 1995.

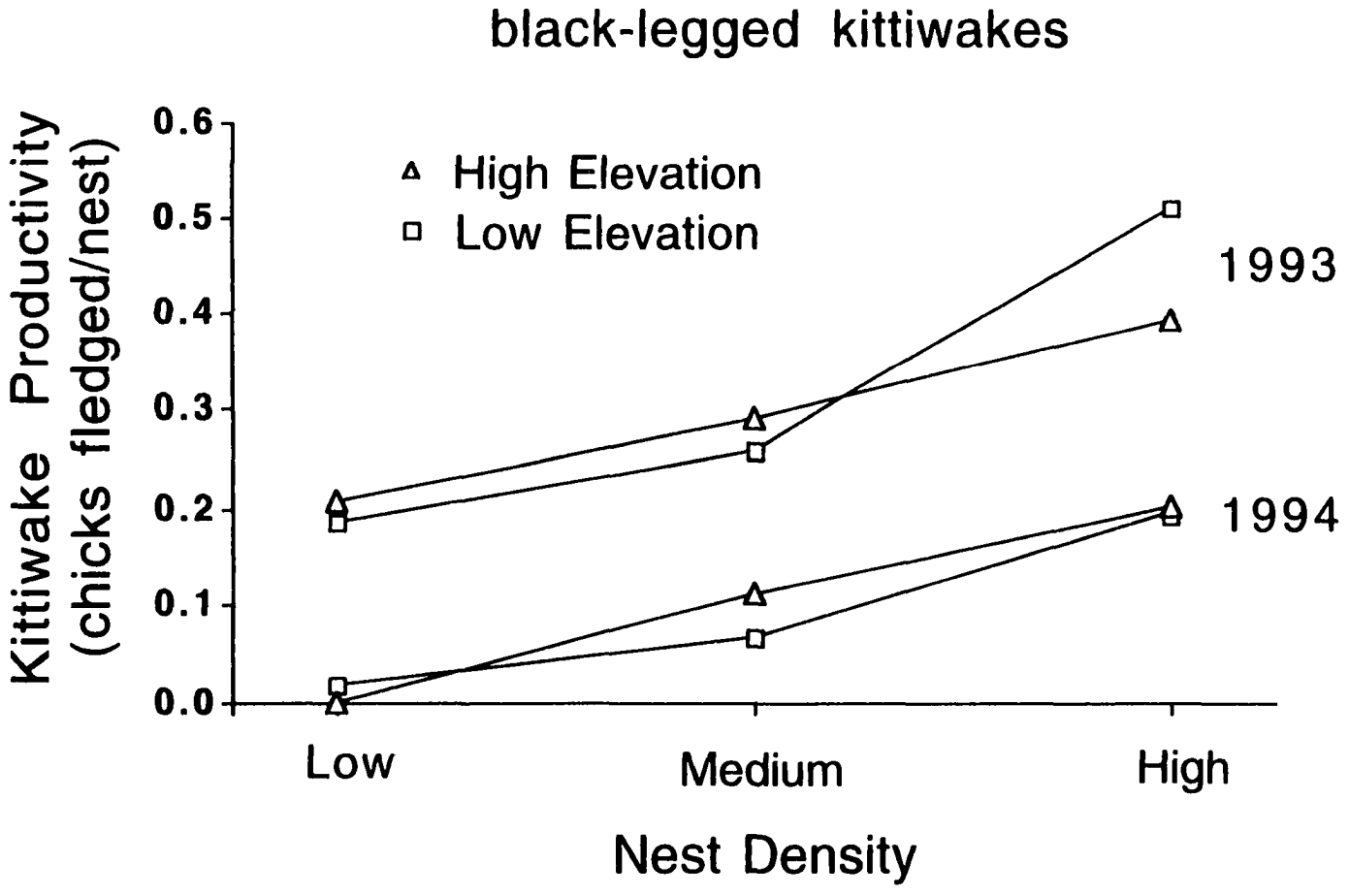



Figure 4.3. Within-island patterns of black-legged kittiwake productivity. Productivity was greater on high-density plots in both years, but did not differ between high- and low-elevation plots in either year.

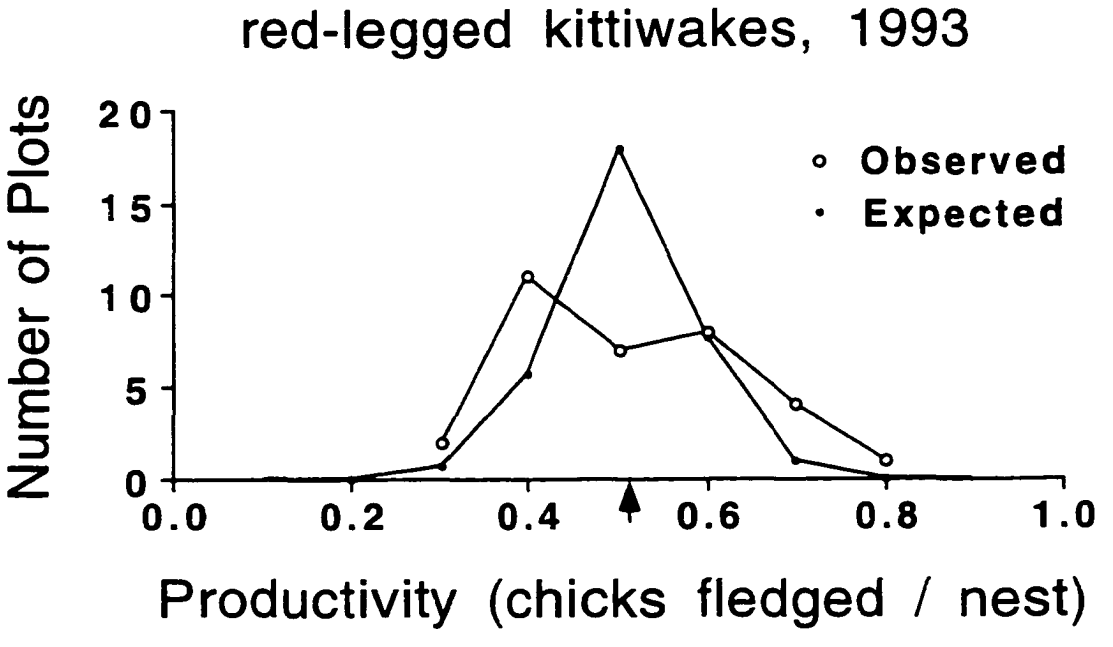



Figure 4.4. Observed and expected distributions of red-legged kittiwake productivity on plots with similar physical and social characteristics. Data are from 1993 for 33 plots that were north-facing, high-elevation, high-density, > 50% red-legged kittiwake in species composition, and contained > 40 nests / plot. Observed values were over-distributed relative to the expected distribution because nests within plots shared a common reproductive fate to a greater degree than expected by chance. Arrow denotes mean productivity of these plots.

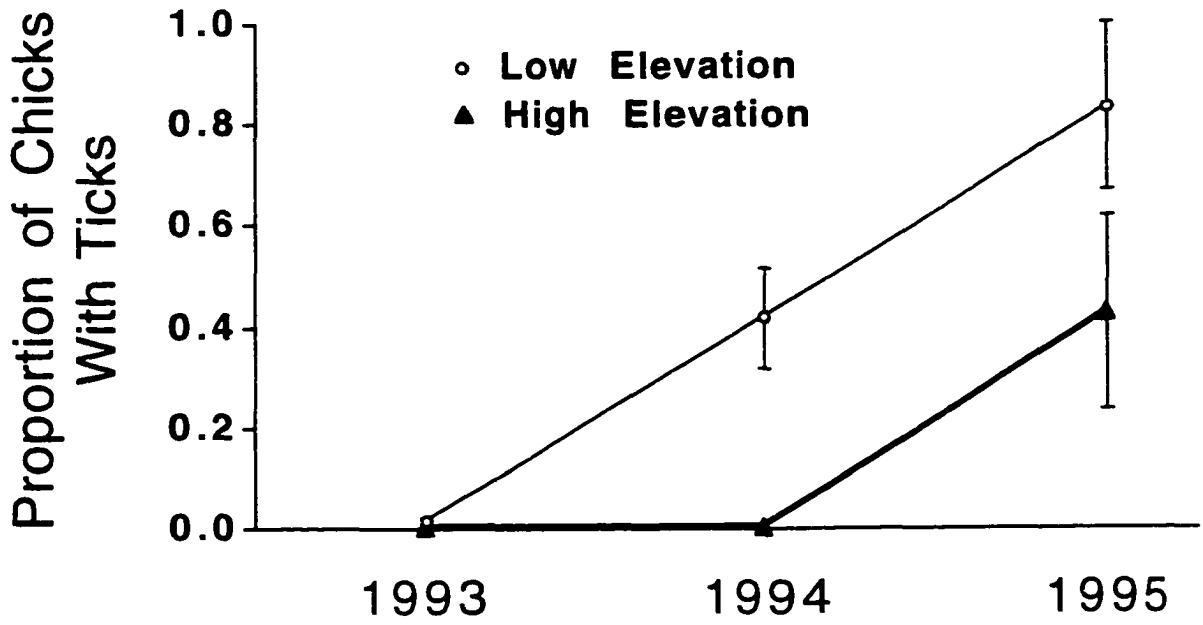



Figure 4.5. Patterns of tick infestation of kittiwake chicks. Tick infestation (proportion of chicks with ticks) increased significantly across years and was highest overall at low elevations. Data for both kittiwake species pooled in this analysis.

## GENERAL CONCLUSIONS

The estimated breeding population of red-legged kittiwakes on St. George Island (194,000 individuals) comprises more than 80% of the estimated global breeding population of this species. Furthermore, red-legged kittiwakes are not uniformly distributed within St. George Island, rather, they are concentrated within the "High Bluff" area where they experience enhanced reproductive performance. As a consequence, this 4 km stretch of high-elevation cliffs is the core breeding area for red-legged kittiwakes on St. George Island and is critical breeding habitat for the species as a whole. Therefore, precautions should be taken to protect the High Bluff area from human disturbance during the kittiwake breeding season (May - September).

I found that the nesting distribution of red-legged kittiwakes on St. George Island is not shaped by competitive displacement by larger-bodied black-legged kittiwakes: rather, nest site preferences differ markedly between species (Red-legged kittiwakes prefer narrow ledges, black-legged kittiwakes prefer wide ledges and both species prefer ledges located in areas where conspecifics nest at high density), and nest sites are not limiting to either species (kittiwake populations have declined by 30-40% over the past 20 years on St. George Island). Although competitive displacement does not currently shape the nesting distribution of kittiwakes, interspecific competition may have shaped nest-site preferences at some time during the evolutionary history of these two species. Therefore, current nest-site preferences and resource partitioning of kittiwakes may be a "ghost of competition past".

Food shortage and poor productivity are currently believed to have caused population declines of kittiwakes in the early 1980's on St. George Island (Hatch et al. 1993); however, factors affecting the food supply and productivity of kittiwakes are poorly understood at present. I found that weather explained between 34% and 68% of inter-annual variability in kittiwake reproduction: kittiwakes bred earlier and had better reproductive performance in summers preceded by colder winters with more extensive

sea ice cover. Surprisingly, kittiwake productivity was poorly related to weather conditions during the actual breeding season. These results suggest that winter weather has an indirect effect on kittiwake reproduction by affecting the distribution and abundance of kittiwake prey the following summer. In contrast, reduced growth rates of kittiwake chicks exposed to strong winds and differences between the two species in effects of wind on chick growth, suggest that weather can directly affect breeding kittiwakes via energetic demands of thermoregulation and foraging efficiency of adults.

In addition to interannual variability, kittiwakes on St. George Island exhibited two marked spatial patterns of within-colony variability in productivity: variability among areas (the "High Bluff" effect) and variability among plots sharing similar characteristics (the "Within Area" effect). Traditional hypotheses for within-colony variability (food abundance, localized predators, weather, parasites and disease, information centers, social facilitation) do not explain these patterns. Two possible explanations, localized "Bird Quality" and "Information Neighborhoods", are complex but generate exclusive predictions which can be experimentally tested.

I have not answered the "big picture" questions regarding population declines and poor, variable productivity of kittiwakes on St. George Island. I can't explain why populations declined or why they stabilized. Although food abundance is generally believed to drive productivity and populations of seabirds, little it known about factors regulating prey populations and the availability of prey to surface-feeding seabirds. Furthermore, although prey availability may explain inter-annual variability in kittiwake productivity, it can't explain substantial with-colony variability observed on St. George Island. The main strength and drawback of the scientific method is that it advances our understanding of complex patterns through the gradual accumulation of facts, small bits of information. Although my research has not answered the "big picture" questions, it has contributed substantially to our understanding of factors affecting populations and productivity of the little-studied red-legged kittiwake, and its ecological relationship to

the more widespread and better studied black-legged kittiwake.

## LITERATURE CITED

Baird, P. H. 1994. Black-legged Kittiwake (*Rissa tridactyla*). Pages 1-26 *in* A. Poole and F. Gill, editors. The birds of North America, no. 92. Academy of Natural Sciences of Philadelphia and American Ornithologists' Union, Philadelphia, Pennsylvania, USA.

Byrd, G. V., and J. C. Williams. 1993. Red-legged Kittiwake (*Rissa brevirostris*). Pages 1-11 *in* A. Poole and F. Gill, editors. The birds of North America, no. 60. Academy of Natural Sciences of Philadelphia and American Ornithologists' Union, Philadelphia, Pennsylvania, USA.

Byrd, G. V., Williams, J. C., Artukhin, Y.B., and Vyatkin, P.S. 1997. Trends in populations of Red-legged Kittiwake (*Rissa brevirostris*), a Bering Sea endemic. Bird Conservation International. 7:167-180.

Cullen, E. 1957. Adaptations in the kittiwake to cliff-nesting. Ibis 99:275-302.

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt. 1993. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. Pages 140-153 *in* K. T. Briggs, K. H. Morgan, and D. Seigel-Causey, editors. The status, ecology, and conservation of marine birds in the north Pacific. Canadian Wildlife Service Special Publication. Ottawa, Canada.

Hickey, J. J., and F. L. Craighead. 1977. A census of seabirds on the Pribilof Islands. U. S. Department of Commerce, NOAA, OCSEAP, Final Report 2:96-195.

Merrick, R. L., T. R. Loughlin, and D. G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumatopias jubatus*, in Alaska, 1956-86. Fisheries Bulletin 85:351-365.

Pitcher, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulana richardsi*, on Tugidak Island, Gulf of Alaska. Marine Mammal Science 6:121-134.

Squibb, R. C., and G. L. Hunt. 1983. A comparison of nesting-ledges used by seabirds on St. George Island. Ecology 64:727-734.

York, A. E., and P. Kozloff. 1987. On the estimation of the numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980-86. Fisheries Bulletin 85:367-375.

Appendix A. Raw counts for whole-island census photos in 1995.

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Village | 1 | m48-3 | 2 | July 30 | 1900 | 0 | 0 |
| Village | 1 | m48-2 | 2 | July 30 | 1900 | 7 | 11 |
| Village | 1 | m47-25 | 2 | July 30 | 1903 | 11 | 8 |
| Village | 1 | m47-23 | 2 | July 30 | 1903 | 112 | 8 |
| Village | 1 | m47-22 | 2 | July 30 | 1906 | 71 | 1 |
| Village | 1 | m47-21 | 2 | July 30 | 1909 | 3 | 3 |
| Village | 1 | m48-4 | 2 | July 30 | 1909 | 0 | 0 |
| Village | 1 | m48-5 | 3 | July 30 | 1912 | 0 | 8 |
| Village | 1 | m48-7 | 3 | July 30 | 1912 | 0 | 2 |
| Village | 1 | m48-8 | 1 | July 30 | 1915 | 22 | 20 |
| Village | 1 | m48-9 | 2 | July 30 | 1915 | 28 | 47 |
| Village | 1 | m48-10 | 1 | July 30 | 1918 | 53 | 18 |
| Village | 1 | m48-11 | 2 | July 30 | 1918 | 56 | 32 |
| Village | 1 | m48-13 | 2 | July 30 | 1921 | 12 | 6 |
| Village | 1 | m48-14 | 2 | July 30 | 1921 | 19 | 1 |
| Village | 1 | m48-15 | 2 | July 30 | 1924 | 58 | 4 |
| Village | 1 | m48-16 | 2 | July 30 | 1924 | 0 | 0 |
| Village | 1 | m48-17 | 2 | July 30 | 1927 | 0 | 0 |
| Village | 1 | m47-2 | 2 | July 30 | 1927 | 13 | 2 |
| Village | 1 | m47-3 | 2 | July 30 | 1930 | 30 | 1 |
| Village | 1 | m47-4 | 2 | July 30 | 1930 | 11 | 1 |
| Village | 1 | m47-5 | 3 | July 30 | 1933 | 24 | 1 |
| Village | 1 | m47-7 | 3 | July 30 | 1933 | 61 | 2 |
| Village | 1 | m47-8 | 3 | July 30 | 1936 | 170 | 0 |
| Village | 1 | m47-9 | 3 | July 30 | 1936 | 82 | 0 |
| Village | 1 | m47-10 | 3 | July 30 | 1939 | 20 | 2 |
| Village | 1 | m47-11 | 3 | July 30 | 1939 | 67 | 1 |
| Village | 1 | m47-13 | 2 | July 30 | 1942 | 55 | 3 |
| Village | 1 | m47-14 | 1 | July 30 | 1942 | 71 | 0 |
| Village | 1 | m47-15 | 2 | July 30 | 1945 | 58 | 0 |
| Village | 1 | m47-16 | 2 | July 30 | 1945 | 55 | 1 |
| Village | 1 | m47-17 | 2 | July 30 | 1948 | 131 | 1 |
| Village | 1 | m47-19 | 2 | July 30 | 1948 | 12 | 0 |
| Village | 1 | m47-20 | 2 | July 30 | 1951 | 0 | 0 |
| Village | 1 | m45-19 | 2 | July 30 | 1951 | 0 | 0 |
| Village | 1 | m45-20 | 2 | July 30 | 1914 | 0 | 0 |
| Village | 1 | m45-21 | 2 | July 30 | 1954 | 0 | 0 |
| Village | 1 | m45-22 | 2 | July 30 | 1957 | 28 | 0 |
| Village | 1 | m45-23 | 2 | July 30 | 1957 | 26 | 2 |
| Village | 1 | m45-25 | 2 | July 30 | 2000 | 60 | 0 |
| Village | 1 | m46-2 | 2 | July 30 | 2000 | 46 | 0 |
| Village | 1 | m46-3 | 1 | July 30 | 2003 | 60 | 0 |
| Village | 1 | m46-9 | 2 | July 30 | 2003 | 3 | 0 |
| Village | 1 | m46-4 | 2 | July 30 | 2006 | 112 | 0 |
| Village | 1 | m46-5 | 2 | July 30 | 2006 | 47 | 1 |
| Village | 1 | m46-7 | 2 | July 30 | 2009 | 3 | 0 |
| Village | 1 | m46-8 | 2 | July 30 | 2009 | 2 | 3 |

[a] 1 = 0 - 91.5 m, 2 = >91.5 m - 180 m, 3 = > 180 m.

[b] 1 = sharp, 2 = good, 3 = blurred.

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Village | 1 | m46-10 | 2 | July 30 | 2012 | 3 | 0 |
| Village | 1 | m46-16 | 2 | July 30 | 2012 | 0 | 0 |
| Village | 1 | m46-15 | 2 | July 30 | 2015 | 71 | 5 |
| Village | 1 | m46-14 | 2 | July 30 | 2015 | 125 | 16 |
| Village | 1 | m46-13 | 2 | July 30 | 2018 | 5 | 1 |
| Village | 1 | m46-11 | 2 | July 30 | 2018 | 30 | 19 |
| Village | 1 | m46-17 | 2 | July 30 | 2021 | 0 | 0 |
| Village | 1 | m46-19 | 2 | July 30 | 2021 | 39 | 0 |
| Village | 1 | m46-20 | 2 | July 30 | 2024 | 2 | 0 |
| Village | 1 | m46-21 | 2 | July 30 | 2024 | 8 | 22 |
| Village | 1 | m46-22 | 2 | July 30 | 2027 | 62 | 36 |
| Village | 1 | m46-23 | 2 | July 30 | 2027 | 32 | 0 |
| Village | 1 | m46-25 | 2 | July 30 | 2030 | 0 | 0 |
| First Bluff | 1 | m26-11 | 2 | July 30 | 1215 | 0 | 0 |
| First Bluff | 1 | m26-13 | 2 | July 30 | 1218 | 0 | 0 |
| First Bluff | 1 | m26-14 | 1 | July 30 | 1221 | 28 | 5 |
| First Bluff | 1 | m26-15 | 1 | July 30 | 1224 | 133 | 53 |
| First Bluff | 1 | m26-16 | 1 | July 30 | 1227 | 69 | 55 |
| First Bluff | 2 | m26-19 | 1 | July 30 | 1230 | 128 | 7 |
| First Bluff | 1 | m26-17 | 1 | July 30 | 1231 | 122 | 69 |
| First Bluff | 2 | m26-20 | 1 | July 30 | 1232 | 171 | 43 |
| First Bluff | 1 | m26-21 | 2 | July 30 | 1233 | 66 | 48 |
| First Bluff | 2 | m27-2 | 3 | July 30 | 1234 | 134 | 62 |
| First Bluff | 1 | m26-22 | 2 | July 30 | 1235 | 146 | 147 |
| First Bluff | 2 | m27-3 | 3 | July 30 | 1236 | 16 | 14 |
| First Bluff | 1 | m26-23 | 2 | July 30 | 1237 | 243 | 131 |
| First Bluff | 2 | m27-4 | 3 | July 30 | 1238 | 89 | 20 |
| First Bluff | 1 | m26-25 | 2 | July 30 | 1239 | 648 | 40 |
| First Bluff | 2 | m27-13 | 2 | July 30 | 1240 | 35 | 20 |
| First Bluff | 2 | m27-9 | 1 | July 30 | 1241 | 544 | 63 |
| First Bluff | 1 | m27-5 | 1 | July 30 | 1242 | 273 | 38 |
| First Bluff | 2 | m27-10 | 1 | July 30 | 1243 | 261 | 32 |
| First Bluff | 1 | m27-7 | 1 | July 30 | 1244 | 203 | 127 |
| First Bluff | 2 | m27-11 | 1 | July 30 | 1245 | 85 | 2 |
| First Bluff | 1 | m27-8 | 1 | July 30 | 1246 | 112 | 142 |
| First Bluff | 2 | m27-19 | 1 | July 30 | 1247 | 265 | 53 |
| First Bluff | 1 | m27-14 | 1 | July 30 | 1248 | 76 | 13 |
| First Bluff | 2 | m27-20 | 1 | July 30 | 1249 | 599 | 46 |
| First Bluff | 1 | m27-15 | 1 | July 30 | 1250 | 31 | 14 |
| First Bluff | 2 | m27-21 | 1 | July 30 | 1251 | 224 | 151 |
| First Bluff | 1 | m27-16 | 1 | July 30 | 1252 | 127 | 223 |
| First Bluff | 2 | m27-22 | 1 | July 30 | 1253 | 185 | 42 |
| First Bluff | 1 | m27-17 | 1 | July 30 | 1254 | 158 | 231 |
| First Bluff | 1 | m27-23 | 1 | July 30 | 1255 | 143 | 151 |
| First Bluff | 1 | m27-25 | 1 | July 30 | 1256 | 120 | 106 |
| First Bluff | 1 | m28-2 | 1 | July 30 | 1257 | 237 | 307 |
| First Bluff | 1 | m28-3 | 1 | July 30 | 1258 | 272 | 125 |
| First Bluff | 1 | m28-4 | 3 | July 30 | 1259 | 194 | 86 |
| First Bluff | 1 | m28-7 | 3 | July 30 | 1300 | 135 | 195 |
| First Bluff | 1 | m28-8 | 2 | July 30 | 1301 | 187 | 179 |
| First Bluff | 1 | m28-9 | 2 | July 30 | 1302 | 214 | 274 |
| High Bluff | 2 | m28-16 | 2 | July 30 | 1303 | 331 | 118 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clanty [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| High Bluff | 1 | m28-10 | 3 | July 30 | 1304 | 117 | 210 |
| High Bluff | 2 | m28-17 | 2 | July 30 | 1305 | 354 | 354 |
| High Bluff | 1 | m28-11 | 3 | July 30 | 1306 | 122 | 219 |
| High Bluff | 2 | m28-19 | 3 | July 30 | 1307 | 223 | 227 |
| High Bluff | 1 | m28-13 | 1 | July 30 | 1308 | 115 | 225 |
| High Bluff | 2 | m28-20 | 3 | July 30 | 1309 | 298 | 178 |
| High Bluff | 1 | m28-14 | 2 | July 30 | 1310 | 102 | 175 |
| High Bluff | 3 | m36-17 | 1 | July 30 | 1539 | 421 | 11 |
| High Bluff | 2 | m28-21M | 2 | July 30 | 1310 | 434 | 255 |
| High Bluff | 1 | m28-15 | 1 | July 30 | 1311 | 185 | 67 |
| High Bluff | 3 | m36-16 | 2 | July 30 | 1538 | 269 | 3 |
| High Bluff | 2 | m29-2M | 2 | July 30 | 1312 | 435 | 436 |
| High Bluff | 1 | m28-22 | 1 | July 30 | 1313 | 82 | 260 |
| High Bluff | 3 | m36-15U | 2 | July 30 | 1537 | 123 | 11 |
| High Bluff | 2 | m36-15M | 2 | July 30 | 1537 | 408 | 74 |
| High Bluff | 2 | m29-3 | 2 | July 30 | 1314 | 129 | 10 |
| High Bluff | 1 | m28-23 | 2 | July 30 | 1315 | 90 | 222 |
| High Bluff | 3 | m36-14U | 2 | July 30 | 1536 | 358 | 16 |
| High Bluff | 2 | m36-14M | 1 | July 30 | 1536 | 244 | 138 |
| High Bluff | 1 | m28-25 | 2 | July 30 | 1316 | 138 | 215 |
| High Bluff | 3 | m36-13U | 2 | July 30 | 1535 | 160 | 7 |
| High Bluff | 2 | m36-13M | 2 | July 30 | 1535 | 286 | 80 |
| High Bluff | 3 | m36-5 | 2 | July 30 | 1534 | 391 | 15 |
| High Bluff | 3 | m36-11U | 2 | July 30 | 1533 | 99 | 2 |
| High Bluff | 2 | m36-11M | 2 | July 30 | 1533 | 286 | 65 |
| High Bluff | 2 | m36-22 | 2 | July 30 | 1540 | 350 | 83 |
| High Bluff | 1 | m36-19 | 2 | July 30 | 1541 | 98 | 257 |
| High Bluff | 3 | m36-4U | 2 | July 30 | 1532 | 197 | 11 |
| High Bluff | 2 | m36-4M | 2 | July 30 | 1532 | 117 | 26 |
| High Bluff | 3 | m36-3U | 2 | July 30 | 1531 | 288 | 25 |
| High Bluff | 2 | m36-3M | 2 | July 30 | 1531 | 170 | 26 |
| High Bluff | 2 | m36-23 | 2 | July 30 | 1542 | 559 | 291 |
| High Bluff | 1 | m36-20 | 2 | July 30 | 1543 | 102 | 320 |
| High Bluff | 3 | m35-16U | 2 | July 30 | 1530 | 699 | 95 |
| High Bluff | 2 | m35-16M | 2 | July 30 | 1530 | 355 | 87 |
| High Bluff | 2 | m36-25 | 1 | July 30 | 1544 | 441 | 158 |
| High Bluff | 1 | m36-21 | 2 | July 30 | 1545 | 68 | 151 |
| High Bluff | 3 | m36-2 | 2 | July 30 | 1545 | 87 | 3 |
| High Bluff | 3 | m35-15U | 2 | July 30 | 1529 | 420 | 17 |
| High Bluff | 2 | m35-15M | 2 | July 30 | 1529 | 183 | 1 |
| High Bluff | 2 | m38-5 | 2 | July 30 | 1543 | 314 | 46 |
| High Bluff | 1 | m38-2 | 2 | July 30 | 1547 | 105 | 88 |
| High Bluff | 3 | m35-9 | 2 | July 30 | 1528 | 186 | 0 |
| High Bluff | 3 | m36-9 | 3 | July 30 | 1528 | 91 | 8 |
| High Bluff | 3 | m35-22U | 1 | July 30 | 1527 | 61 | 0 |
| High Bluff | 2 | m35-22M | 2 | July 30 | 1557 | 351 | 40 |
| High Bluff | 2 | m38-7 | 2 | July 30 | 1548 | 582 | 356 |
| High Bluff | 1 | m38-3 | 3 | July 30 | 1549 | 57 | 103 |
| High Bluff | 3 | m35-21U | 2 | July 30 | 1526 | 203 | 3 |
| High Bluff | 2 | m35-21M | 2 | July 30 | 1526 | 223 | 26 |
| High Bluff | 2 | m38-8 | 2 | July 30 | 1550 | 111 | 66 |
| High Bluff | 1 | m38-4 | 2 | July 30 | 1551 | 118 | 41 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| High Bluff | 3 | m35-23 | 3 | July 30 | 1525 | 437 | 2 |
| High Bluff | 3 | m35-8U | 2 | July 30 | 1524 | 857 | 6 |
| High Bluff | 2 | m35-8M | 2 | July 30 | 1524 | 343 | 12 |
| High Bluff | 2 | m38-14 | 3 | July 30 | 1552 | 481 | 103 |
| High Bluff | 1 | m38-9 | 2 | July 30 | 1553 | 175 | 183 |
| High Bluff | 3 | m35-20 | 2 | July 30 | 1523 | 149 | 0 |
| High Bluff | 3 | m35-7U | 2 | July 30 | 1522 | 1665 | 63 |
| High Bluff | 2 | m35-7M | 2 | July 30 | 1522 | 816 | 13 |
| High Bluff | 2 | m38-15 | 3 | July 30 | 1554 | 467 | 69 |
| High Bluff | 1 | m38-10 | 2 | July 30 | 1555 | 114 | 130 |
| High Bluff | 3 | m35-5U | 3 | July 30 | 1521 | 217 | 0 |
| High Bluff | 2 | m35-5M | 3 | July 30 | 1521 | 600 | 9 |
| High Bluff | 3 | m35-19 | 1 | July 30 | 1520 | 2027 | 38 |
| High Bluff | 2 | m38-16 | 2 | July 30 | 1556 | 600 | 56 |
| High Bluff | 1 | m38-11 | 2 | July 30 | 1557 | 154 | 19 |
| High Bluff | 3 | m35-4 | 3 | July 30 | 1519 | 1770 | 30 |
| High Bluff | 3 | m35-13U | 3 | July 30 | 1518 | 1438 | 4 |
| High Bluff | 2 | m35-13M | 3 | July 30 | 1518 | 237 | 1 |
| High Bluff | 2 | m38-17 | 3 | July 30 | 1558 | 232 | 26 |
| High Bluff | 1 | m38-13 | 2 | July 30 | 1559 | 167 | 31 |
| High Bluff | 1 | m38-19 | 3 | July 30 | 1600 | 61 | 2 |
| High Bluff | 3 | m35-3U | 3 | July 30 | 1517 | 1038 | 17 |
| High Bluff | 2 | m35-3M | 3 | July 30 | 1517 | 197 | 9 |
| High Bluff | 2 | m38-25 | 2 | July 30 | 1601 | 594 | 67 |
| High Bluff | 1 | m38-20 | 3 | July 30 | 1602 | 49 | 0 |
| High Bluff | 3 | m35-2U | 3 | July 30 | 1516 | 1131 | 0 |
| High Bluff | 2 | m35-2M | 3 | July 30 | 1516 | 90 | 0 |
| High Bluff | 3 | m34-14 | 3 | July 30 | 1515 | 1149 | 0 |
| High Bluff | 2 | m39-2 | 1 | July 30 | 1603 | 459 | 20 |
| High Bluff | 1 | m38-21 | 2 | July 30 | 1604 | 26 | 0 |
| High Bluff | 3 | m34-25 | 1 | July 30 | 1514 | 2942 | 14 |
| High Bluff | 3 | m34-13 | 3 | July 30 | 1513 | 228 | 0 |
| High Bluff | 3 | m35-10 | 3 | July 30 | 1512 | 350 | 0 |
| High Bluff | 2 | m39-5 | 1 | July 30 | 1605 | 351 | 5 |
| High Bluff | 1 | m38-22 | 2 | July 30 | 1606 | 52 | 1 |
| High Bluff | 3 | m34-23 | 2 | July 30 | 1511 | 1970 | 2 |
| High Bluff | 2 | m39-4 | 1 | July 30 | 1607 | 0 | 0 |
| High Bluff | 1 | m38-23 | 3 | July 30 | 1608 | 114 | 30 |
| High Bluff | 3 | m34-20 | 3 | July 30 | 1510 | 858 | 36 |
| High Bluff | 3 | m34-9 | 3 | July 30 | 1509 | 1571 | 53 |
| High Bluff | 2 | m39-7 | 2 | July 30 | 1609 | 152 | 5 |
| High Bluff | 2 | m39-14 | 3 | July 30 | 1610 | 722 | 137 |
| High Bluff | 1 | m39-8 | 2 | July 30 | 1611 | 106 | 3 |
| High Bluff | 1 | m39-9 | 3 | July 30 | 1612 | 52 | 7 |
| High Bluff | 3 | m34-19 | 2 | July 30 | 1508 | 439 | 9 |
| High Bluff | 3 | m34-22 | 3 | July 30 | 1507 | 1678 | 8 |
| High Bluff | 2 | m39-15 | 3 | July 30 | 1613 | 631 | 56 |
| High Bluff | 1 | m39-10 | 3 | July 30 | 1614 | 25 | 0 |
| High Bluff | 3 | m34-8 | 3 | July 30 | 1506 | 1685 | 36 |
| High Bluff | 3 | m34-7 | 3 | July 30 | 1505 | 2239 | 63 |
| High Bluff | 2 | m39-16 | 3 | July 30 | 1615 | 339 | 34 |
| High Bluff | 1 | m39-11 | 3 | July 30 | 1616 | 70 | 1 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| High Bluff | 1 | m39-13 | 3 | July 30 | 1617 | 39 | 2 |
| High Bluff | 3 | m34-16 | 2 | July 30 | 1504 | 887 | 54 |
| High Bluff | 3 | m34-21 | 2 | July 30 | 1503 | 120 | 5 |
| High Bluff | 3 | m34-5 | 3 | July 30 | 1502 | 1069 | 58 |
| High Bluff | 3 | m34-15 | 2 | July 30 | 1501 | 617 | 59 |
| High Bluff | 2 | m39-17 | 3 | July 30 | 1618 | 796 | 90 |
| High Bluff | 2 | m39-20 | 3 | July 30 | 1619 | 314 | 21 |
| High Bluff | 1 | m39-22 | 3 | July 30 | 1620 | 364 | 139 |
| High Bluff | 3 | m33-20 | 2 | July 30 | 1550 | 342 | 0 |
| High Bluff | 3 | m34-10 | 2 | July 30 | 1459 | 378 | 0 |
| High Bluff | 3 | m34-4 | 3 | July 30 | 1458 | 51 | 0 |
| High Bluff | 2 | m40-8 | 2 | July 30 | 1621 | 792 | 1 |
| High Bluff | 1 | m39-23 | 3 | July 30 | 1622 | 243 | 369 |
| High Bluff | 3 | m34-3 | 3 | July 30 | 1458 | 246 | 0 |
| High Bluff | 3 | m33-19 | 2 | July 30 | 1457 | 192 | 0 |
| High Bluff | 3 | m34-11 | 2 | July 30 | 1457 | 870 | 0 |
| High Bluff | 2 | m40-9 | 1 | July 30 | 1623 | 809 | 1 |
| High Bluff | 1 | m39-25 | 3 | July 30 | 1624 | 570 | 185 |
| High Bluff | 3 | m33-17 | 2 | July 30 | 1456 | 1238 | 263 |
| High Bluff | 2 | m40-10 | 1 | July 30 | 1625 | 1057 | 164 |
| High Bluff | 1 | m40-4 | 2 | July 30 | 1626 | 158 | 46 |
| High Bluff | 1 | m40-5 | 2 | July 30 | 1627 | 187 | 127 |
| High Bluff | 3 | m33-25 | 3 | July 30 | 1456 | 605 | 58 |
| High Bluff | 3 | m33-16 | 2 | July 30 | 1455 | 330 | 0 |
| High Bluff | 2 | m40-11 | 2 | July 30 | 1628 | 880 | 43 |
| High Bluff | 2 | m39-21 | 3 | July 30 | 1629 | 627 | 3 |
| High Bluff | 1 | m40-7 | 2 | July 30 | 1630 | 157 | 210 |
| High Bluff | 3 | m33-15 | 1 | July 30 | 1455 | 1108 | 8 |
| High Bluff | 3 | m33-23 | 2 | July 30 | 1454 | 1534 | 126 |
| High Bluff | 2 | m40-19 | 1 | July 30 | 1631 | 822 | 6 |
| High Bluff | 1 | m40-14 | 2 | July 30 | 1632 | 176 | 87 |
| High Bluff | 3 | m33-10 | 3 | July 30 | 1454 | 1582 | 141 |
| High Bluff | 3 | m40-13 | 2 | July 30 | 1633 | 923 | 5 |
| High Bluff | 2 | m40-20 | 1 | July 30 | 1634 | 553 | 1 |
| High Bluff | 1 | m40-15 | 1 | July 30 | 1635 | 127 | 13 |
| High Bluff | 3 | m33-9 | 2 | July 30 | 1453 | 1950 | 279 |
| High Bluff | 2 | m40-21 | 2 | July 30 | 1636 | 557 | 11 |
| High Bluff | 1 | m40-16 | 2 | July 30 | 1637 | 133 | 58 |
| High Bluff | 3 | m33-21U | 3 | July 30 | 1453 | 791 | 82 |
| High Bluff | 2 | m33-21M | 3 | July 30 | 1452 | 98 | 13 |
| High Bluff | 3 | m33-8 | 2 | July 30 | 1452 | 467 | 3 |
| High Bluff | 2 | m40-22 | 2 | July 30 | 1638 | 709 | 14 |
| High Bluff | 1 | m40-17 | 2 | July 30 | 1639 | 109 | 46 |
| High Bluff | 3 | m33-14 | 2 | July 30 | 1451 | 36 | 0 |
| High Bluff | 3 | m33-7 | 2 | July 30 | 1451 | 563 | 8 |
| High Bluff | 3 | m33-5 | 2 | July 30 | 1450 | 617 | 6 |
| High Bluff | 3 | m33-13 | 2 | July 30 | 1450 | 132 | 4 |
| High Bluff | 2 | m41-4 | 2 | July 30 | 1640 | 701 | 64 |
| High Bluff | 2 | m41-5 | 2 | July 30 | 1641 | 831 | 125 |
| High Bluff | 2 | m41-7 | 2 | July 30 | 1642 | 970 | 105 |
| High Bluff | 1 | m40-23 | 1 | July 30 | 1643 | 71 | 2 |
| High Bluff | 1 | m40-25 | 2 | July 30 | 1644 | 35 | 1 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| High Bluff | 1 | m41-2 | 2 | July 30 | 1645 | 2 | 0 |
| High Bluff | 1 | m41-3 | 2 | July 30 | 1646 | 0 | 0 |
| High Bluff | 3 | m33-4 | 2 | July 30 | 1449 | 2099 | 89 |
| High Bluff | 2 | m41-8 | 2 | July 30 | 1647 | 457 | 208 |
| High Bluff | 1 | m41-9 | 2 | July 30 | 1647 | 115 | 0 |
| High Bluff | 3 | m33-3 | 1 | July 30 | 1448 | 892 | 179 |
| High Bluff | 3 | m32-23 | 1 | July 30 | 1447 | 1012 | 12 |
| High Bluff | 2 | m41-14 | 2 | July 30 | 1648 | 357 | 110 |
| High Bluff | 2 | m41-15 | 2 | July 30 | 1648 | 426 | 142 |
| High Bluff | 1 | m41-10 | 2 | July 30 | 1649 | 112 | 71 |
| High Bluff | 3 | m32-16 | 3 | July 30 | 1446 | 462 | 0 |
| High Bluff | 3 | m32-22 | 2 | July 30 | 1445 | 961 | 44 |
| High Bluff | 3 | m32-2 | 2 | July 30 | 1445 | 98 | 0 |
| High Bluff | 2 | m41-16 | 2 | July 30 | 1649 | 528 | 79 |
| High Bluff | 1 | m41-11 | 2 | July 30 | 1650 | 133 | 158 |
| High Bluff | 1 | m41-13 | 2 | July 30 | 1650 | 169 | 33 |
| High Bluff | 3 | m32-21 | 2 | July 30 | 1443 | 1304 | 7 |
| High Bluff | 3 | m32-15 | 2 | July 30 | 1443 | 976 | 25 |
| High Bluff | 2 | m42-2 | 2 | July 30 | 1651 | 566 | 92 |
| High Bluff | 2 | m42-3 | 1 | July 30 | 1651 | 581 | 15 |
| High Bluff | 1 | m41-20 | 2 | July 30 | 1652 | 77 | 1 |
| High Bluff | 1 | m41-21 | 1 | July 30 | 1652 | 361 | 12 |
| High Bluff | 3 | m32-14 | 3 | July 30 | 1442 | 745 | 1 |
| High Bluff | 3 | m32-20 | 3 | July 30 | 1442 | 283 | 0 |
| High Bluff | 2 | m42-4 | 1 | July 30 | 1653 | 556 | 6 |
| High Bluff | 1 | m41-22 | 2 | July 30 | 1653 | 125 | 4 |
| High Bluff | 3 | m32-11 | 2 | July 30 | 1441 | 644 | 25 |
| High Bluff | 3 | m32-9 | 2 | July 30 | 1440 | 309 | 0 |
| High Bluff | 3 | m32-19 | 1 | July 30 | 1440 | 97 | 0 |
| High Bluff | 2 | m42-5 | 2 | July 30 | 1654 | 314 | 10 |
| High Bluff | 2 | m41-19 | 1 | July 30 | 1654 | 101 | 0 |
| High Bluff | 1 | m41-23 | 2 | July 30 | 1655 | 97 | 2 |
| High Bluff | 2 | m42-7 | 2 | July 30 | 1655 | 90 | 0 |
| High Bluff | 2 | m41-17 | 3 | July 30 | 1656 | 78 | 0 |
| High Bluff | 1 | m41-25 | 2 | July 30 | 1656 | 160 | 100 |
| High Bluff | 2 | m42-11 | 2 | July 30 | 1657 | 101 | 17 |
| High Bluff | 1 | m42-8 | 1 | July 30 | 1658 | 80 | 119 |
| High Bluff | 2 | m42-10 | 2 | July 30 | 1659 | 79 | 1 |
| High Bluff | 1 | m42-9 | 2 | July 30 | 1700 | 165 | 128 |
| Needle Rock | 1 | m42-13 | 2 | July 30 | 1701 | 165 | 117 |
| Needle Rock | 1 | m42-14 | 2 | July 30 | 1702 | 206 | 219 |
| Needle Rock | 1 | m42-15 | 2 | July 30 | 1703 | 219 | 143 |
| Needle Rock | 1 | m42-16 | 2 | July 30 | 1704 | 176 | 85 |
| Needle Rock | 1 | m42-17 | 2 | July 30 | 1705 | 197 | 88 |
| Needle Rock | 1 | m42-19 | 2 | July 30 | 1706 | 440 | 21 |
| Needle Rock | 1 | m42-20 | 2 | July 30 | 1707 | 344 | 16 |
| Needle Rock | 1 | m42-22 | 1 | July 30 | 1708 | 257 | 36 |
| Needle Rock | 1 | m42-23 | 2 | July 30 | 1709 | 117 | 38 |
| Needle Rock | 1 | m42-25 | 2 | July 30 | 1710 | 218 | 214 |
| Needle Rock | 1 | m43-2 | 2 | July 30 | 1711 | 211 | 242 |
| Needle Rock | 1 | m43-3 | 2 | July 30 | 1712 | 415 | 176 |
| Needle Rock | 2 | m43-14 | 1 | July 30 | 1713 | 269 | 104 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Needle Rock | 1 | m43-8 | 2 | July 30 | 1714 | 981 | 163 |
| Needle Rock | 2 | m43-15 | 2 | July 30 | 1715 | 981 | 163 |
| Needle Rock | 1 | m43-9 | 3 | July 30 | 1716 | 189 | 110 |
| Needle Rock | 1 | m43-19 | 2 | July 30 | 1717 | 72 | 23 |
| Needle Rock | 1 | m43-5 | 1 | July 30 | 1718 | 138 | 61 |
| Needle Rock | 2 | m43-20 | 2 | July 30 | 1719 | 111 | 0 |
| Needle Rock | 2 | m43-16 | 2 | July 30 | 1720 | 1134 | 133 |
| Needle Rock | 2 | m43-4 | 1 | July 30 | 1721 | 158 | 6 |
| Needle Rock | 1 | m43-10 | 2 | July 30 | 1722 | 122 | 15 |
| Needle Rock | 2 | m43-17 | 2 | July 30 | 1723 | 341 | 94 |
| Needle Rock | 1 | m43-13 | 3 | July 30 | 1724 | 37 | 102 |
| Needle Rock | 1 | m43-11 | 2 | July 30 | 1725 | 233 | 235 |
| Needle Rock | 2 | m44-7 | 2 | July 30 | 1726 | 49 | 23 |
| Needle Rock | 1 | m44-9 | 1 | July 30 | 1727 | 108 | 14 |
| Needle Rock | 1 | m44-5 | 2 | July 30 | 1728 | 227 | 172 |
| Needle Rock | 2 | m44-10 | 2 | July 30 | 1729 | 66 | 0 |
| Needle Rock | 2 | m45-17 | 2 | July 30 | 1730 | 216 | 14 |
| Needle Rock | 2 | m44-8 | 1 | July 30 | 1731 | 741 | 42 |
| Needle Rock | 2 | m44-4 | 2 | July 30 | 1732 | 2392 | 40 |
| Needle Rock | 1 | m43-25 | 2 | July 30 | 1733 | 223 | 122 |
| Needle Rock | 2 | m44-3 | 2 | July 30 | 1734 | 2646 | 84 |
| Needle Rock | 1 | m43-23 | 2 | July 30 | 1735 | 267 | 46 |
| Needle Rock | 2 | m43-21 | 3 | July 30 | 1736 | 217 | 4 |
| Needle Rock | 2 | m44-2 | 2 | July 30 | 1737 | 1552 | 29 |
| Needle Rock | 1 | m43-22 | 1 | July 30 | 1738 | 422 | 1 |
| Needle Rock | 1 | m44-11 | 2 | July 30 | 1739 | 223 | 94 |
| Needle Rock | 2 | m2-18 | 3 | July 15 | 1626 | 156 | 42 |
| Needle Rock | 1 | m44-13 | 2 | July 30 | 1740 | 255 | 169 |
| Needle Rock | 2 | m2-16 | 3 | July 15 | 1624 | 91 | 44 |
| Needle Rock | 1 | m44-14 | 3 | July 30 | 1741 | 162 | 65 |
| Needle Rock | 2 | m2-15 | 3 | July 15 | 1622 | 115 | 18 |
| Needle Rock | 1 | m44-15 | 2 | July 30 | 1742 | 103 | 7 |
| Needle Rock | 2 | m2-14 | 2 | July 15 | 1620 | 6 | 0 |
| Needle Rock | 1 | m44-16 | 2 | July 30 | 1743 | 323 | 35 |
| Needle Rock | 2 | m2-13 | 2 | July 15 | 1618 | 0 | 0 |
| Needle Rock | 1 | m44-17 | 2 | July 30 | 1744 | 228 | 62 |
| Needle Rock | 2 | m2-12 | 2 | July 15 | 1616 | 17 | 16 |
| Needle Rock | 1 | m44-19 | 2 | July 30 | 1745 | 248 | 59 |
| Needle Rock | 2 | m2-10 | 2 | July 15 | 1614 | 54 | 28 |
| Needle Rock | 1 | m44-20 | 2 | July 30 | 1746 | 556 | 117 |
| Needle Rock | 2 | m2-9 | 2 | July 15 | 1612 | 109 | 58 |
| Needle Rock | 1 | m44-21 | 1 | July 30 | 1747 | 504 | 19 |
| Needle Rock | 2 | m2-8 | 2 | July 15 | 1610 | 120 | 49 |
| Needle Rock | 1 | m44-22 | 1 | July 30 | 1748 | 223 | 47 |
| Needle Rock | 2 | m2-7 | 2 | July 15 | 1608 | 412 | 41 |
| Needle Rock | 1 | m44-23 | 2 | July 30 | 1749 | 315 | 70 |
| Needle Rock | 2 | m2-6 | 3 | July 15 | 1606 | 100 | 115 |
| Needle Rock | 1 | m44-25 | 1 | July 30 | 1750 | 285 | 32 |
| Needle Rock | 2 | m2-4 | 3 | July 15 | 1604 | 323 | 106 |
| Needle Rock | 1 | m45-2 | 2 | July 30 | 1751 | 286 | 83 |
| Needle Rock | 2 | m2-3 | 3 | July 15 | 1602 | 213 | 33 |
| Needle Rock | 1 | m45-3 | 2 | July 30 | 1752 | 313 | 239 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Needle Rock | 2 | m2-2 | 3 | July 15 | 1600 | 16 | 25 |
| Needle Rock | 1 | m45-4 | 2 | July 30 | 1753 | 136 | 93 |
| Needle Rock | 1 | m45-11 | 3 | July 30 | 1754 | 190 | 21 |
| Needle Rock | 1 | m45-5 | 2 | July 30 | 1755 | 259 | 80 |
| Needle Rock | 2 | m2-19 | 2 | July 15 | 1630 | 0 | 4 |
| Needle Rock | 1 | m45-7 | 2 | July 30 | 1756 | 143 | 159 |
| Needle Rock | 2 | m2-20 | 2 | July 15 | 1632 | 0 | 0 |
| Needle Rock | 1 | m45-8 | 2 | July 30 | 1757 | 185 | 102 |
| Needle Rock | 2 | m2-21 | 3 | July 15 | 1634 | 5 | 35 |
| Needle Rock | 1 | m45-9 | 2 | July 30 | 1758 | 120 | 53 |
| Needle Rock | 2 | m2-22 | 3 | July 15 | 1636 | 179 | 148 |
| Needle Rock | 1 | m45-10 | 2 | July 30 | 1759 | 113 | 152 |
| Needle Rock | 2 | m2-24 | 2 | July 15 | 1638 | 36 | 141 |
| Needle Rock | 1 | m45-13 | 2 | July 30 | 1800 | 102 | 59 |
| Needle Rock | 2 | m2-23 | 2 | July 15 | 1640 | 22 | 97 |
| Needle Rock | 1 | m45-14 | 2 | July 30 | 1801 | 67 | 99 |
| Needle Rock | 2 | m2-7 | 2 | July 15 | 1642 | 123 | 7 |
| Needle Rock | 1 | m45-15 | 2 | July 30 | 1802 | 173 | 24 |
| Needle Rock | 2 | m32-5 | 2 | July 30 | 1803 | 413 | 23 |
| Needle Rock | 2 | m32-4 | 2 | July 30 | 1804 | 374 | 34 |
| Needle Rock | 2 | m32-3 | 2 | July 30 | 1805 | 149 | 60 |
| Needle Rock | 1 | m45-16 | 2 | July 30 | 1806 | 123 | 10 |
| Needle Rock | 1 | m31-25 | 1 | July 30 | 1807 | 226 | 13 |
| Needle Rock | 1 | m31-23 | 1 | July 30 | 1808 | 93 | 0 |
| Needle Rock | 1 | m32-2 | 2 | July 30 | 1809 | 160 | 14 |
| Dalnoi | 2 | m31-22 | 2 | July 30 | 1430 | 94 | 43 |
| Dalnoi | 1 | m31-20 | 2 | July 30 | 1429 | 103 | 67 |
| Dalnoi | 2 | m31-17 | 3 | July 30 | 1428 | 103 | 189 |
| Dalnoi | 1 | m31-19 | 2 | July 30 | 1427 | 106 | 115 |
| Dalnoi | 2 | m31-16 | 2 | July 30 | 1426 | 372 | 347 |
| Dalnoi | 1 | m31-11 | 2 | July 30 | 1425 | 4 | 59 |
| Dalnoi | 2 | m31-15 | 2 | July 30 | 1424 | 485 | 228 |
| Dalnoi | 1 | m31-10 | 2 | July 30 | 1423 | 21 | 9 |
| Dalnoi | 2 | m31-14 | 2 | July 30 | 1422 | 344 | 73 |
| Dalnoi | 2 | m31-8 | 1 | July 30 | 1421 | 151 | 11 |
| Dalnoi | 1 | m31-9 | 2 | July 30 | 1420 | 121 | 23 |
| Dalnoi | 1 | m31-4 | 3 | July 30 | 1419 | 26 | 36 |
| Dalnoi | 2 | m31-7 | 2 | July 30 | 1418 | 166 | 17 |
| Dalnoi | 1 | m31-3 | 2 | July 30 | 1417 | 0 | 0 |
| Dalnoi | 2 | m31-5 | 2 | July 30 | 1416 | 834 | 177 |
| Dalnoi | 1 | m31-2 | 2 | July 30 | 1415 | 0 | 0 |
| Dalnoi | 2 | m30-22 | 2 | July 30 | 1414 | 573 | 109 |
| Dalnoi | 1 | m30-25 | 2 | July 30 | 1413 | 46 | 13 |
| Dalnoi | 2 | m30-21 | 2 | July 30 | 1412 | 600 | 261 |
| Dalnoi | 1 | m30-23 | 2 | July 30 | 1410 | 163 | 69 |
| Dalnoi | 2 | m30-20 | 3 | July 30 | 1409 | 210 | 203 |
| Dalnoi | 1 | m30-15 | 3 | July 30 | 1408 | 141 | 110 |
| Dalnoi | 2 | m30-19 | 3 | July 30 | 1407 | 608 | 570 |
| Dalnoi | 1 | m30-14 | 3 | July 30 | 1406 | 31 | 155 |
| Dalnoi | 2 | m30-17 | 3 | July 30 | 1405 | 537 | 595 |
| Dalnoi | 1 | m30-13 | 3 | July 30 | 1404 | 93 | 102 |
| Dalnoi | 2 | m30-16 | 3 | July 30 | 1403 | 483 | 529 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Dalnoi | 1 | m30-11 | 2 | July 30 | 1402 | 26 | 21 |
| Dalnoi | 2 | m30-10 | 2 | July 30 | 1401 | 519 | 506 |
| Dalnoi | 1 | m30-7 | 2 | July 30 | 1400 | 94 | 73 |
| Dalnoi | 2 | m30-9 | 2 | July 30 | 1359 | 471 | 273 |
| Dalnoi | 1 | m30-5 | 2 | July 30 | 1358 | 168 | 45 |
| Dalnoi | 2 | m30-8 | 2 | July 30 | 1357 | 679 | 194 |
| Dalnoi | 1 | m30-4 | 2 | July 30 | 1356 | 99 | 95 |
| Dalnoi | 2 | m30-3 | 2 | July 30 | 1355 | 669 | 285 |
| Dalnoi | 1 | m29-23 | 3 | July 30 | 1354 | 111 | 55 |
| Dalnoi | 2 | m30-2 | 2 | July 30 | 1353 | 674 | 374 |
| Dalnoi | 1 | m29-22 | 3 | July 30 | 1352 | 95 | 78 |
| Dalnoi | 2 | m29-25 | 3 | July 30 | 1351 | 339 | 373 |
| Dalnoi | 1 | m29-21 | 3 | July 30 | 1350 | 30 | 24 |
| Dalnoi | 1 | m29-20 | 3 | July 30 | 1349 | 0 | 4 |
| Dalnoi | 2 | m29-19 | 1 | July 30 | 1348 | 565 | 226 |
| Dalnoi | 1 | m29-15 | 2 | July 30 | 1347 | 133 | 184 |
| Dalnoi | 2 | m29-17 | 1 | July 30 | 1346 | 640 | 128 |
| Dalnoi | 1 | m29-14 | 2 | July 30 | 1345 | 189 | 185 |
| Dalnoi | 2 | m29-16 | 2 | July 30 | 1344 | 458 | 171 |
| Dalnoi | 1 | m29-13 | 2 | July 30 | 1343 | 124 | 89 |
| Dalnoi | 2 | m29-11 | 2 | July 30 | 1342 | 308 | 121 |
| Dalnoi | 1 | m29-7 | 2 | July 30 | 1341 | 0 | 0 |
| Dalnoi | 2 | m29-10 | 2 | July 30 | 1340 | 366 | 78 |
| Dalnoi | 1 | m29-5 | 3 | July 30 | 1339 | 110 | 17 |
| Fox Castle | 1 | m21-14 | 3 | July 27 | 1745 | 17 | 12 |
| Fox Castle | 1 | m21-15 | 3 | July 27 | 1746 | 54 | 131 |
| Fox Castle | 1 | m21-16 | 3 | July 27 | 1747 | 125 | 192 |
| Fox Castle | 1 | m21-17 | 3 | July 27 | 1747 | 157 | 305 |
| Fox Castle | 1 | m21-19 | 2 | July 27 | 1748 | 50 | 268 |
| Fox Castle | 2 | m21-21 | 2 | July 27 | 1749 | 31 | 120 |
| Fox Castle | 1 | m21-20 | 2 | July 27 | 1750 | 131 | 167 |
| Fox Castle | 2 | m22-4 | 3 | July 27 | 1750 | 45 | 79 |
| Fox Castle | 1 | m21-22 | 2 | July 27 | 1751 | 12 | 85 |
| Fox Castle | 2 | m22-5 | 3 | July 27 | 1752 | 157 | 108 |
| Fox Castle | 1 | m21-23 | 3 | July 27 | 1753 | 129 | 11 |
| Fox Castle | 2 | m22-7 | 3 | July 27 | 1753 | 140 | 253 |
| Fox Castle | 1 | m21-25 | 2 | July 27 | 1754 | 195 | 119 |
| Fox Castle | 2 | m22-8 | 3 | July 27 | 1755 | 83 | 468 |
| Fox Castle | 1 | m22-2 | 3 | July 27 | 1756 | 35 | 344 |
| Fox Castle | 2 | m22-9 | 3 | July 27 | 1756 | 157 | 412 |
| Fox Castle | 1 | m22-3 | 3 | July 27 | 1757 | 40 | 191 |
| Fox Castle | 2 | m22-10 | 3 | July 27 | 1758 | 360 | 1003 |
| Fox Castle | 1 | m22-11 | 2 | July 27 | 1759 | 136 | 141 |
| Fox Castle | 2 | m22-15 | 3 | July 27 | 1759 | 91 | 69 |
| Fox Castle | 1 | m22-13 | 2 | July 27 | 1800 | 95 | 246 |
| Fox Castle | 2 | m23-7 | 3 | July 27 | 1801 | 464 | 16 |
| Fox Castle | 1 | m23-8 | 2 | July 27 | 1802 | 66 | 11 |
| Fox Castle | 2 | m22-16 | 2 | July 27 | 1802 | 41 | 29 |
| Fox Castle | 1 | m22-14 | 2 | July 27 | 1803 | 253 | 339 |
| Fox Castle | 2 | m22-21 | 2 | July 27 | 1804 | 115 | 63 |
| Fox Castle | 2 | m23-9 | 2 | July 27 | 1805 | 70 | 2 |
| Fox Castle | 1 | m22-17 | 3 | July 27 | 1805 | 132 | 47 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Fox Castle | 2 | m22-22 | 2 | July 27 | 1806 | 117 | 11 |
| Fox Castle | 1 | m22-19 | 3 | July 27 | 1807 | 26 | 93 |
| Fox Castle | 2 | m22-23 | 2 | July 27 | 1808 | 88 | 21 |
| Fox Castle | 1 | m22-20 | 2 | July 27 | 1808 | 88 | 52 |
| Fox Castle | 2 | m23-10 | 2 | July 27 | 1809 | 55 | 17 |
| Fox Castle | 2 | m22-25 | 2 | July 27 | 1810 | 169 | 25 |
| Fox Castle | 1 | m23-11 | 2 | July 27 | 1811 | 38 | 1 |
| Fox Castle | 1 | m23-3 | 2 | July 27 | 1811 | 63 | 11 |
| Fox Castle | 2 | m23-2 | 3 | July 27 | 1812 | 163 | 132 |
| Fox Castle | 1 | m23-4 | 2 | July 27 | 1813 | 83 | 118 |
| Fox Castle | 2 | m23-15 | 3 | July 27 | 1814 | 253 | 18 |
| Fox Castle | 2 | m23-17 | 3 | July 27 | 1814 | 375 | 17 |
| Fox Castle | 1 | m23-5 | 2 | July 27 | 1815 | 93 | 94 |
| Fox Castle | 1 | m23-16 | 2 | July 27 | 1816 | 128 | 54 |
| Fox Castle | 2 | m23-13 | 3 | July 27 | 1817 | 223 | 39 |
| Fox Castle | 2 | m23-14 | 2 | July 27 | 1817 | 129 | 22 |
| Fox Castle | 1 | m23-19 | 2 | July 27 | 1818 | 181 | 161 |
| Fox Castle | 2 | m23-22 | 3 | July 27 | 1819 | 113 | 88 |
| Fox Castle | 1 | m23-20 | 3 | July 27 | 1820 | 92 | 86 |
| Fox Castle | 1 | m23-21 | 3 | July 27 | 1820 | 46 | 39 |
| Fox Castle | 2 | m24-2 | 3 | July 27 | 1821 | 279 | 69 |
| Fox Castle | 2 | m24-3 | 3 | July 27 | 1822 | 80 | 2 |
| Fox Castle | 1 | m23-23 | 2 | July 27 | 1823 | 169 | 147 |
| Fox Castle | 1 | m23-25 | 2 | July 27 | 1823 | 138 | 56 |
| Fox Castle | 2 | m24-9 | 2 | July 27 | 1824 | 142 | 118 |
| Fox Castle | 1 | m24-5 | 2 | July 27 | 1825 | 88 | 30 |
| Fox Castle | 2 | m24-10 | 2 | July 27 | 1826 | 154 | 143 |
| Fox Castle | 1 | m24-7 | 2 | July 27 | 1826 | 42 | 2 |
| Fox Castle | 2 | m24-11 | 3 | July 27 | 1827 | 116 | 114 |
| Fox Castle | 1 | m24-8 | 3 | July 27 | 1828 | 41 | 12 |
| Fox Castle | 2 | m24-19 | 2 | July 27 | 1829 | 69 | 48 |
| Fox Castle | 2 | m24-20 | 2 | July 27 | 1829 | 107 | 69 |
| Fox Castle | 1 | m24-13 | 2 | July 27 | 1830 | 101 | 117 |
| Fox Castle | 1 | m24-14 | 2 | July 27 | 1831 | 54 | 39 |
| Fox Castle | 1 | m24-15 | 2 | July 27 | 1832 | 19 | 36 |
| Fox Castle | 2 | m24-21 | 2 | July 27 | 1832 | 97 | 119 |
| Fox Castle | 1 | m24-16 | 1 | July 27 | 1833 | 96 | 124 |
| Fox Castle | 2 | m24-22 | 2 | July 27 | 1834 | 49 | 121 |
| Fox Castle | 1 | m24-17 | 2 | July 27 | 1835 | 0 | 0 |
| Fox Castle | 2 | m25-4 | 2 | July 27 | 1835 | 36 | 46 |
| Fox Castle | 1 | m24-23 | 2 | July 27 | 1836 | 24 | 25 |
| Fox Castle | 2 | m25-5 | 2 | July 27 | 1837 | 75 | 166 |
| Fox Castle | 1 | m24-25 | 2 | July 27 | 1838 | 5 | 1 |
| Fox Castle | 2 | m25-7 | 2 | July 27 | 1839 | 201 | 82 |
| Fox Castle | 1 | m25-2 | 2 | July 27 | 1839 | 1 | 0 |
| Fox Castle | 2 | m25-8 | 2 | July 27 | 1840 | 102 | 37 |
| Fox Castle | 1 | m25-3 | 2 | July 27 | 1841 | 77 | 115 |
| Fox Castle | 2 | m25-14 | 2 | July 27 | 1842 | 230 | 161 |
| Fox Castle | 1 | m25-9 | 3 | July 27 | 1842 | 18 | 108 |
| Fox Castle | 2 | m25-15 | 2 | July 27 | 1843 | 133 | 113 |
| Fox Castle | 1 | m25-10 | 3 | July 27 | 1844 | 4 | 10 |
| Fox Castle | 2 | m25-16 | 2 | July 27 | 1845 | 135 | 93 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Fox Castle | 1 | m25-11 | 3 | July 27 | 1846 | 5 | 53 |
| Fox Castle | 2 | m25-17 | 2 | July 27 | 1846 | 35 | 7 |
| Fox Castle | 1 | m25-13 | 2 | July 27 | 1847 | 4 | 188 |
| Fox Castle | 2 | m25-22 | 2 | July 27 | 1848 | 86 | 5 |
| Fox Castle | 1 | m25-19 | 2 | July 27 | 1849 | 0 | 6 |
| Fox Castle | 2 | m25-23 | 2 | July 27 | 1849 | 96 | 27 |
| Fox Castle | 1 | m25-20 | 2 | July 27 | 1850 | 6 | 5 |
| Fox Castle | 2 | m25-25 | 2 | July 27 | 1851 | 1852 | 6 |
| Fox Castle | 1 | m25-21 | 2 | July 27 | 1852 | 25 | 20 |
| Fox Castle | 2 | m26-4 | 3 | July 27 | 1853 | 29 | 19 |
| Fox Castle | 1 | m26-2 | 2 | July 27 | 1854 | 1 | 1 |
| Fox Castle | 2 | m26-5 | 3 | July 27 | 1855 | 139 | 69 |
| Fox Castle | 1 | m26-3 | 3 | July 27 | 1855 | 11 | 115 |
| Zapadni | 1 | m5-4 | 2 | July 23 | 1300 | 0 | 0 |
| Zapadni | 1 | m5-5 | 2 | July 23 | 1303 | 0 | 0 |
| Zapadni | 1 | m5-7 | 2 | July 23 | 1306 | 0 | 1 |
| Zapadni | 1 | m5-8 | 2 | July 23 | 1309 | 0 | 1 |
| Zapadni | 1 | m5-9 | 2 | July 23 | 1312 | 0 | 0 |
| Zapadni | 1 | m5-10 | 3 | July 23 | 1315 | 1 | 0 |
| Zapadni | 1 | m5-11 | 3 | July 23 | 1318 | 1 | 2 |
| Zapadni | 1 | m5-13 | 2 | July 23 | 1321 | 8 | 2 |
| Zapadni | 1 | m5-14 | 2 | July 23 | 1324 | 6 | 2 |
| Zapadni | 1 | m5-15 | 2 | July 23 | 1327 | 20 | 4 |
| Zapadni | 1 | m5-16 | 2 | July 23 | 1330 | 55 | 12 |
| Zapadni | 1 | m5-17 | 2 | July 23 | 1333 | 5 | 1 |
| Zapadni | 1 | m5-19 | 2 | July 23 | 1336 | 7 | 19 |
| Zapadni | 1 | m5-20 | 2 | July 23 | 1339 | 9 | 6 |
| Zapadni | 1 | m5-21 | 2 | July 23 | 1342 | 0 | 0 |
| Zapadni | 1 | m5-22 | 2 | July 23 | 1345 | 0 | 0 |
| Zapadni | 1 | m5-23 | 2 | July 23 | 1348 | 0 | 0 |
| Zapadni | 1 | m5-25 | 2 | July 23 | 1351 | 26 | 35 |
| Zapadni | 1 | gap#1 | 2 | July 23 | 1421 | 162 | 141 |
| Zapadni | 1 | m6-16 | 3 | July 23 | 1424 | 2 | 5 |
| Zapadni | 1 | m6-17 | 3 | July 23 | 1427 | 11 | 28 |
| Zapadni | 1 | m6-19 | 3 | July 23 | 1430 | 55 | 59 |
| Zapadni | 1 | m6-20 | 3 | July 23 | 1433 | 25 | 43 |
| Zapadni | 1 | m6-21 | 2 | July 23 | 1436 | 48 | 31 |
| Zapadni | 1 | m6-22 | 2 | July 23 | 1439 | 4 | 4 |
| Zapadni | 1 | m6-23 | 2 | July 23 | 1442 | 25 | 17 |
| Zapadni | 1 | m6-25 | 2 | July 23 | 1445 | 51 | 22 |
| Zapadni | 1 | m7-3 | 3 | July 23 | 1447 | 61 | 62 |
| Zapadni | 1 | m7-4 | 3 | July 23 | 1450 | 22 | 71 |
| Zapadni | 1 | m7-5 | 2 | July 23 | 1453 | 61 | 60 |
| Zapadni | 1 | m7-7 | 2 | July 23 | 1456 | 82 | 61 |
| Zapadni | 1 | m7-8 | 2 | July 23 | 1459 | 31 | 59 |
| Zapadni | 1 | m7-9 | 2 | July 23 | 1502 | 24 | 30 |
| Zapadni | 1 | m7-10 | 2 | July 23 | 1505 | 39 | 34 |
| Zapadni | 1 | m7-11 | 2 | July 23 | 1508 | 26 | 38 |
| Zapadni | 1 | m7-13 | 2 | July 23 | 1511 | 91 | 61 |
| Zapadni | 1 | m7-14 | 3 | July 23 | 1514 | 15 | 22 |
| Zapadni | 1 | m7-15 | 3 | July 23 | 1517 | 12 | 65 |
| Zapadni | 1 | m7-16 | 2 | July 23 | 1520 | 34 | 96 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Zapadni | 1 | m7-17 | 2 | July 23 | 1523 | 42 | 50 |
| Zapadni | 1 | m7-19 | 2 | July 23 | 1526 | 65 | 43 |
| Zapadni | 1 | m7-20 | 2 | July 23 | 1529 | 7 | 61 |
| Zapadni | 1 | m7-21 | 2 | July 23 | 1532 | 5 | 57 |
| Zapadni | 1 | m7-22 | 2 | July 23 | 1535 | 21 | 30 |
| Zapadni | 1 | m7-23 | 2 | July 23 | 1538 | 48 | 54 |
| Zapadni | 1 | m7-25 | 2 | July 23 | 1541 | 17 | 56 |
| Zapadni | 1 | m8-2 | 3 | July 23 | 1544 | 55 | 62 |
| Zapadni | 1 | m8-3 | 3 | July 23 | 1547 | 13 | 67 |
| Red Bluff | 1 | m17-20 | 2 | July 27 | 1600 | 170 | 172 |
| Red Bluff | 1 | m17-21 | 2 | July 27 | 1601 | 232 | 180 |
| Red Bluff | 1 | m17-22 | 2 | July 27 | 1602 | 145 | 32 |
| Red Bluff | 1 | m17-23 | 2 | July 27 | 1603 | 166 | 63 |
| Red Bluff | 1 | m17-25 | 2 | July 27 | 1604 | 129 | 82 |
| Red Bluff | 1 | m18-2 | 2 | July 27 | 1605 | 241 | 86 |
| Red Bluff | 1 | m18-3 | 2 | July 27 | 1606 | 86 | 131 |
| Red Bluff | 1 | m18-4 | 2 | July 27 | 1607 | 179 | 92 |
| Red Bluff | 1 | m18-5 | 2 | July 27 | 1608 | 399 | 179 |
| Red Bluff | 1 | m18-7 | 2 | July 27 | 1609 | 90 | 157 |
| Red Bluff | 1 | m18-8 | 2 | July 27 | 1610 | 151 | 153 |
| Red Bluff | 1 | m18-9 | 2 | July 27 | 1611 | 319 | 198 |
| Red Bluff | 1 | m18-10 | 2 | July 27 | 1612 | 116 | 208 |
| Red Bluff | 1 | m18-11 | 2 | July 27 | 1613 | 178 | 174 |
| Red Bluff | 1 | m18-13 | 2 | July 27 | 1614 | 256 | 227 |
| Red Bluff | 1 | m18-14 | 2 | July 27 | 1615 | 516 | 270 |
| Red Bluff | 1 | m18-15 | 2 | July 27 | 1616 | 148 | 250 |
| Red Bluff | 1 | m18-16 | 2 | July 27 | 1617 | 581 | 205 |
| Red Bluff | 1 | m18-17 | 2 | July 27 | 1618 | 508 | 157 |
| Red Bluff | 1 | m18-19 | 2 | July 27 | 1619 | 336 | 270 |
| Red Bluff | 1 | m18-20 | 2 | July 27 | 1620 | 356 | 338 |
| Red Bluff | 1 | m18-21 | 2 | July 27 | 1621 | 222 | 268 |
| Red Bluff | 1 | m18-22 | 3 | July 27 | 1622 | 81 | 308 |
| Red Bluff | 1 | m18-23 | 3 | July 27 | 1623 | 177 | 170 |
| Red Bluff | 1 | m18-25 | 2 | July 27 | 1624 | 200 | 347 |
| Red Bluff | 1 | m19-2 | 2 | July 27 | 1625 | 229 | 229 |
| Red Bluff | 1 | m19-3 | 2 | July 27 | 1626 | 270 | 302 |
| Red Bluff | 1 | m19-4 | 2 | July 27 | 1627 | 149 | 219 |
| Red Bluff | 1 | m19-5 | 2 | July 27 | 1628 | 177 | 254 |
| Red Bluff | 1 | m19-7 | 2 | July 27 | 1629 | 93 | 106 |
| Red Bluff | 1 | m19-8 | 3 | July 27 | 1630 | 263 | 222 |
| Red Bluff | 1 | m19-9 | 3 | July 27 | 1631 | 324 | 159 |
| Red Bluff | 1 | m19-10 | 2 | July 27 | 1632 | 232 | 239 |
| Red Bluff | 1 | m19-11 | 2 | July 27 | 1633 | 203 | 218 |
| Red Bluff | 1 | m19-13 | 2 | July 27 | 1634 | 160 | 220 |
| Red Bluff | 1 | m19-14 | 2 | July 27 | 1635 | 211 | 215 |
| Red Bluff | 1 | m19-15 | 2 | July 27 | 1636 | 85 | 99 |
| Red Bluff | 1 | m19-16 | 2 | July 27 | 1637 | 137 | 138 |
| Red Bluff | 1 | m19-17 | 2 | July 27 | 1638 | 25 | 256 |
| Red Bluff | 1 | m19-19 | 2 | July 27 | 1639 | 35 | 82 |
| Red Bluff | 1 | m19-20 | 2 | July 27 | 1640 | 72 | 142 |
| Red Bluff | 1 | m19-21 | 2 | July 27 | 1641 | 165 | 150 |
| Red Bluff | 1 | m19-25 | 2 | July 27 | 1642 | 28 | 163 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Red Bluff | 1 | m19-22 | 2 | July 27 | 1643 | 87 | 81 |
| Red Bluff | 1 | m20-2 | 3 | July 27 | 1644 | 13 | 88 |
| Red Bluff | 1 | m19-23 | 2 | July 27 | 1645 | 112 | 140 |
| Red Bluff | 1 | m20-8 | 2 | July 27 | 1646 | 35 | 51 |
| Red Bluff | 1 | m20-3 | 2 | July 27 | 1647 | 184 | 49 |
| Red Bluff | 1 | m20-9 | 2 | July 27 | 1648 | 5 | 49 |
| Red Bluff | 1 | m20-14 | 2 | July 27 | 1649 | 57 | 26 |
| Red Bluff | 1 | m20-4 | 2 | July 27 | 1650 | 122 | 55 |
| Red Bluff | 1 | m20-10 | 2 | July 27 | 1651 | 62 | 112 |
| Red Bluff | 1 | m20-5 | 2 | July 27 | 1652 | 17 | 13 |
| Red Bluff | 1 | m20-7 | 2 | July 27 | 1653 | 127 | 35 |
| Red Bluff | 1 | m20-11 | 2 | July 27 | 1654 | 57 | 65 |
| Red Bluff | 1 | m20-13 | 2 | July 27 | 1655 | 21 | 56 |
| Red Bluff | 1 | m20-15 | 2 | July 27 | 1656 | 38 | 75 |
| Red Bluff | 1 | m20-17 | 2 | July 27 | 1657 | 30 | 85 |
| Red Bluff | 1 | m20-16 | 2 | July 27 | 1658 | 191 | 56 |
| Red Bluff | 1 | m20-19 | 2 | July 27 | 1659 | 31 | 116 |
| Red Bluff | 1 | m20-21 | 3 | July 27 | 1700 | 68 | 58 |
| Red Bluff | 1 | m20-20 | 2 | July 27 | 1710 | 25 | 110 |
| Red Bluff | 1 | m20-22 | 3 | July 27 | 1712 | 101 | 84 |
| Red Bluff | 1 | m20-23 | 2 | July 27 | 1723 | 39 | 69 |
| Red Bluff | 1 | m20-25 | 2 | July 27 | 1704 | 84 | 133 |
| Red Bluff | 1 | m21-2 | 3 | July 27 | 1705 | 48 | 113 |
| Red Bluff | 1 | m21-3 | 3 | July 27 | 1706 | 136 | 53 |
| Red Bluff | 1 | m21-4 | 3 | July 27 | 1707 | 143 | 72 |
| Red Bluff | 1 | m21-5 | 3 | July 27 | 1708 | 54 | 112 |
| Red Bluff | 1 | m21-7 | 3 | July 27 | 1709 | 49 | 78 |
| Red Bluff | 1 | m21-8 | 2 | July 27 | 1710 | 87 | 37 |
| Red Bluff | 1 | m21-9 | 2 | July 27 | 1711 | 40 | 26 |
| Red Bluff | 1 | m21-10 | 2 | July 27 | 1712 | 68 | 120 |
| Red Bluff | 1 | m21-11 | 2 | July 27 | 1713 | 40 | 70 |
| Red Bluff | 1 | m9-9 | 3 | July 23 | 1750 | 30 | 86 |
| Red Bluff | 1 | m9-11 | 3 | July 23 | 1748 | 149 | 122 |
| Red Bluff | 1 | m9-8 | 3 | July 23 | 1746 | 192 | 167 |
| Red Bluff | 1 | m9-7 | 3 | July 23 | 1742 | 115 | 144 |
| Red Bluff | 1 | m9-5 | 3 | July 23 | 1740 | 75 | 112 |
| Red Bluff | 1 | m9-4 | 3 | July 23 | 1738 | 88 | 34 |
| Red Bluff | 1 | m9-3 | 2 | July 23 | 1736 | 100 | 56 |
| Red Bluff | 1 | m9-2 | 2 | July 23 | 1734 | 215 | 121 |
| Red Bluff | 1 | m8-25 | 2 | July 23 | 1732 | 71 | 130 |
| Red Bluff | 1 | m8-24 | 2 | July 23 | 1730 | 118 | 36 |
| Red Bluff | 1 | m8-23 | 2 | July 23 | 1728 | 18 | 9 |
| Red Bluff | 1 | m8-20 | 2 | July 23 | 1726 | 3 | 1 |
| Red Bluff | 1 | m8-19 | 2 | July 23 | 1724 | 0 | 0 |
| Red Bluff | 1 | m8-18 | 2 | July 23 | 1722 | 3 | 0 |
| Red Bluff | 1 | m8-17 | 2 | July 23 | 1720 | 30 | 1 |
| Red Bluff | 1 | m8-15 | 2 | July 23 | 1718 | 0 | 0 |
| Red Bluff | 1 | m8-14 | 2 | July 23 | 1716 | 0 | 0 |
| Red Bluff | 1 | m8-13 | 2 | July 23 | 1714 | 8 | 11 |
| Red Bluff | 1 | m8-12 | 1 | July 23 | 1712 | 67 | 11 |
| Red Bluff | 1 | m8-11 | 2 | July 23 | 1710 | 65 | 50 |
| Red Bluff | 1 | m8-9 | 3 | July 23 | 1708 | 82 | 109 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clanty [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Red Bluff | 1 | m8-8 | 3 | July 23 | 1706 | 49 | 56 |
| Red Bluff | 1 | m8-7 | 2 | July 23 | 1704 | 90 | 67 |
| Red Bluff | 1 | m8-6 | 2 | July 23 | 1702 | 193 | 44 |
| Red Bluff | 1 | m8-5 | 2 | July 23 | 1700 | 10 | 1 |
| Garden Cove | 1 | m12-9 | 2 | July 27 | 1257 | 0 | 0 |
| Garden Cove | 1 | m12-10 | 2 | July 27 | 1258 | 1 | 2 |
| Garden Cove | 1 | m12-11 | 2 | July 27 | 1300 | 0 | 0 |
| Garden Cove | 1 | m12-13 | 2 | July 27 | 1301 | 0 | 1 |
| Garden Cove | 1 | m12-14 | 2 | July 27 | 1302 | 0 | 0 |
| Garden Cove | 1 | m12-15 | 2 | July 27 | 1303 | 3 | 0 |
| Garden Cove | 1 | m12-16 | 2 | July 27 | 1305 | 36 | 7 |
| Garden Cove | 1 | m12-17 | 2 | July 27 | 1306 | 2 | 1 |
| Garden Cove | 1 | m12-19 | 2 | July 27 | 1307 | 24 | 2 |
| Garden Cove | 1 | m12-20 | 2 | July 27 | 1308 | 90 | 1 |
| Garden Cove | 1 | m12-21 | 2 | July 27 | 1309 | 40 | 12 |
| Garden Cove | 1 | m12-22 | 2 | July 27 | 1311 | 67 | 40 |
| Garden Cove | 1 | m12-23 | 2 | July 27 | 1312 | 0 | 0 |
| Garden Cove | 1 | m12-25 | 2 | July 27 | 1313 | 0 | 0 |
| Garden Cove | 1 | m13-2 | 2 | July 27 | 1314 | 0 | 0 |
| Garden Cove | 1 | m13-3 | 2 | July 27 | 1316 | 0 | 0 |
| Garden Cove | 1 | m13-4 | 2 | July 27 | 1317 | 0 | 0 |
| Garden Cove | 1 | m13-5 | 2 | July 27 | 1318 | 0 | 0 |
| Garden Cove | 1 | m13-7 | 2 | July 27 | 1319 | 0 | 0 |
| Garden Cove | 1 | m13-8 | 2 | July 27 | 1321 | 0 | 0 |
| Garden Cove | 1 | m13-9 | 2 | July 27 | 1322 | 0 | 0 |
| Garden Cove | 1 | m13-10 | 2 | July 27 | 1323 | 0 | 0 |
| Garden Cove | 1 | m13-11 | 2 | July 27 | 1324 | 0 | 0 |
| Garden Cove | 1 | m13-13 | 2 | July 27 | 1326 | 0 | 0 |
| Garden Cove | 1 | m13-14 | 2 | July 27 | 1327 | 0 | 0 |
| Garden Cove | 1 | m13-15 | 2 | July 27 | 1328 | 0 | 0 |
| Garden Cove | 1 | m13-16 | 2 | July 27 | 1329 | 0 | 0 |
| Garden Cove | 1 | m13-17 | 2 | July 27 | 1331 | 0 | 0 |
| Garden Cove | 1 | m13-19 | 2 | July 27 | 1332 | 0 | 0 |
| Garden Cove | 1 | m13-20 | 2 | July 27 | 1333 | 0 | 0 |
| Garden Cove | 1 | m13-21 | 2 | July 27 | 1334 | 0 | 0 |
| Garden Cove | 1 | m13-22 | 2 | July 27 | 1336 | 4 | 0 |
| Garden Cove | 1 | m13-23 | 2 | July 27 | 1337 | 301 | 82 |
| Garden Cove | 1 | m13-25 | 2 | July 27 | 1338 | 386 | 217 |
| Garden Cove | 1 | m14-2 | 3 | July 27 | 1339 | 290 | 161 |
| Garden Cove | 1 | m14-3 | 3 | July 27 | 1341 | 239 | 112 |
| Garden Cove | 1 | m14-4 | 3 | July 27 | 1342 | 121 | 112 |
| Garden Cove | 1 | m14-5 | 2 | July 27 | 1343 | 147 | 157 |
| Garden Cove | 1 | m14-7 | 2 | July 27 | 1344 | 139 | 89 |
| Garden Cove | 1 | m14-8 | 1 | July 27 | 1346 | 50 | 135 |
| Garden Cove | 1 | m14-9 | 2 | July 27 | 1347 | 149 | 105 |
| Garden Cove | 1 | m14-10 | 2 | July 27 | 1348 | 469 | 135 |
| Garden Cove | 1 | m14-11 | 1 | July 27 | 1349 | 258 | 152 |
| Garden Cove | 1 | m14-13 | 2 | July 27 | 1351 | 298 | 187 |
| Garden Cove | 1 | m14-14 | 2 | July 27 | 1352 | 424 | 100 |
| Garden Cove | 1 | m14-15 | 1 | July 27 | 1353 | 439 | 20 |
| Garden Cove | 1 | m14-17 | 2 | July 27 | 1354 | 100 | 19 |
| Garden Cove | 1 | m14-16 | 2 | July 27 | 1356 | 180 | 43 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Garden Cove | 1 | m14-19 | 2 | July 27 | 1357 | 91 | 46 |
| Garden Cove | 1 | m14-20 | 1 | July 27 | 1358 | 94 | 169 |
| Garden Cove | 1 | m14-21 | 1 | July 27 | 1359 | 15 | 193 |
| Garden Cove | 1 | m14-22 | 1 | July 27 | 1401 | 38 | 141 |
| Garden Cove | 1 | m14-23 | 2 | July 27 | 1402 | 182 | 69 |
| Garden Cove | 1 | m15-8M | 2 | July 27 | 1403 | 2 | 26 |
| Garden Cove | 1 | m15-8L | 2 | July 27 | 1404 | 122 | 49 |
| Garden Cove | 1 | m14-25 | 1 | July 27 | 1406 | 69 | 38 |
| Garden Cove | 1 | m15-9M | 2 | July 27 | 1407 | 5 | 61 |
| Garden Cove | 1 | m15-9L | 2 | July 27 | 1408 | 63 | 55 |
| Garden Cove | 1 | m15-2 | 1 | July 27 | 1409 | 32 | 43 |
| Garden Cove | 1 | m15-10M | 2 | July 27 | 1411 | 4 | 59 |
| Garden Cove | 1 | m15-10L | 2 | July 27 | 1412 | 92 | 53 |
| Garden Cove | 1 | m15-3 | 1 | July 27 | 1413 | 39 | 27 |
| Garden Cove | 1 | m15-11M | 2 | July 27 | 1414 | 36 | 29 |
| Garden Cove | 1 | m15-11L | 2 | July 27 | 1416 | 43 | 28 |
| Garden Cove | 1 | m15-4 | 1 | July 27 | 1417 | 168 | 7 |
| Garden Cove | 1 | m15-13M | 2 | July 27 | 1418 | 3 | 25 |
| Garden Cove | 1 | m15-13L | 2 | July 27 | 1419 | 54 | 59 |
| Garden Cove | 1 | m15-5 | 2 | July 27 | 1420 | 92 | 87 |
| Garden Cove | 1 | m15-14M | 1 | July 27 | 1421 | 2 | 23 |
| Garden Cove | 1 | m15-14L | 2 | July 27 | 1422 | 44 | 60 |
| Garden Cove | 1 | m15-7 | 2 | July 27 | 1423 | 126 | 53 |
| Garden Cove | 1 | m15-20M | 2 | July 27 | 1425 | 1 | 0 |
| Garden Cove | 1 | m15-20L | 2 | July 27 | 1426 | 12 | 100 |
| Garden Cove | 1 | m15-15 | 2 | July 27 | 1427 | 152 | 76 |
| Garden Cove | 1 | m15-21M | 2 | July 27 | 1428 | 0 | 47 |
| Garden Cove | 1 | m15-21L | 2 | July 27 | 1430 | 93 | 68 |
| Garden Cove | 1 | m15-16 | 2 | July 27 | 1431 | 114 | 72 |
| Garden Cove | 1 | m15-22M | 1 | July 27 | 1432 | 4 | 25 |
| Garden Cove | 1 | m15-22L | 2 | July 27 | 1433 | 109 | 59 |
| Garden Cove | 1 | m15-17 | 2 | July 27 | 1435 | 7 | 39 |
| Garden Cove | 1 | m15-23U | 2 | July 27 | 1436 | 40 | 44 |
| Garden Cove | 1 | m15-23L | 2 | July 27 | 1437 | 20 | 65 |
| Garden Cove | 1 | m15-19 | 2 | July 27 | 1438 | 4 | 38 |
| Garden Cove | 1 | m15-25M | 2 | July 27 | 1440 | 0 | 36 |
| Garden Cove | 1 | m15-25L | 2 | July 27 | 1441 | 47 | 224 |
| Garden Cove | 1 | m16-2 | 2 | July 27 | 1442 | 156 | 188 |
| Garden Cove | 1 | m16-3 | 1 | July 27 | 1443 | 196 | 119 |
| Garden Cove | 1 | m16-4 | 1 | July 27 | 1445 | 146 | 136 |
| Garden Cove | 1 | m16-5 | 2 | July 27 | 1446 | 66 | 198 |
| Garden Cove | 1 | m16-7 | 2 | July 27 | 1447 | 16 | 148 |
| Garden Cove | 1 | m16-8 | 2 | July 27 | 1448 | 218 | 141 |
| Garden Cove | 1 | m16-9 | 2 | July 27 | 1450 | 118 | 120 |
| Garden Cove | 1 | m16-10 | 2 | July 27 | 1451 | 160 | 86 |
| Garden Cove | 1 | m16-11 | 2 | July 27 | 1452 | 121 | 128 |
| Garden Cove | 1 | m16-13 | 2 | July 27 | 1453 | 93 | 90 |
| Garden Cove | 1 | m16-14 | 2 | July 27 | 1455 | 196 | 141 |
| Garden Cove | 1 | m16-15 | 2 | July 27 | 1456 | 225 | 206 |
| Garden Cove | 1 | m16-16 | 1 | July 27 | 1457 | 106 | 124 |
| Garden Cove | 1 | m16-17 | 1 | July 27 | 1458 | 46 | 82 |
| Garden Cove | 1 | m16-19 | 1 | July 27 | 1500 | 130 | 34 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Garden Cove | 1 | m16-20 | 1 | July 27 | 1501 | 426 | 10 |
| Garden Cove | 1 | m16-21 | 1 | July 27 | 1502 | 102 | 110 |
| Garden Cove | 1 | m16-22 | 1 | July 27 | 1504 | 22 | 127 |
| Garden Cove | 1 | m16-23 | 2 | July 27 | 1505 | 48 | 173 |
| Garden Cove | 1 | m16-25 | 3 | July 27 | 1506 | 44 | 218 |
| Garden Cove | 1 | gap#2 | 2 | July 27 | 1508 | 516 | 734 |
| Garden Cove | 1 | m17-2 | 1 | July 27 | 1509 | 268 | 221 |
| Garden Cove | 1 | m17-3 | 1 | July 27 | 1510 | 191 | 354 |
| Garden Cove | 1 | m17-4 | 1 | July 27 | 1512 | 428 | 264 |
| Garden Cove | 1 | m17-5 | 1 | July 27 | 1513 | 365 | 275 |
| Garden Cove | 1 | m17-7 | 2 | July 27 | 1514 | 775 | 336 |
| Garden Cove | 1 | m17-8 | 2 | July 27 | 1516 | 300 | 242 |
| Garden Cove | 1 | m17-9 | 2 | July 27 | 1517 | 59 | 90 |
| Garden Cove | 1 | m17-10 | 2 | July 27 | 1518 | 155 | 219 |
| Garden Cove | 1 | m17-11 | 2 | July 27 | 1520 | 58 | 173 |
| Garden Cove | 1 | m17-13 | 2 | July 27 | 1521 | 166 | 411 |
| Garden Cove | 1 | m17-14 | 1 | July 27 | 1522 | 289 | 186 |
| Garden Cove | 1 | m17-15 | 2 | July 27 | 1524 | 391 | 198 |
| Garden Cove | 1 | m17-16 | 2 | July 27 | 1525 | 422 | 337 |
| Garden Cove | 1 | m17-17 | 2 | July 27 | 1526 | 232 | 180 |
| Garden Cove | 1 | m17-19 | 2 | July 27 | 1528 | 68 | 69 |
| Tolstoi | 1 | m9-13 | 2 | July 27 | 1145 | 0 | 0 |
| Tolstoi | 1 | m9-14 | 2 | July 27 | 1146 | 7 | 0 |
| Tolstoi | 1 | m9-15 | 2 | July 27 | 1147 | 32 | 3 |
| Tolstoi | 1 | m9-16 | 1 | July 27 | 1148 | 63 | 1 |
| Tolstoi | 1 | m9-17 | 1 | July 27 | 1150 | 11 | 0 |
| Tolstoi | 1 | m9-19 | 2 | July 27 | 1151 | 30 | 0 |
| Tolstoi | 1 | m9-20 | 2 | July 27 | 1152 | 17 | 0 |
| Tolstoi | 1 | m9-21 | 2 | July 27 | 1153 | 12 | 1 |
| Tolstoi | 1 | m9-22 | 2 | July 27 | 1155 | 0 | 0 |
| Tolstoi | 1 | m9-23 | 2 | July 27 | 1156 | 1 | 0 |
| Tolstoi | 1 | m9-24 | 2 | July 27 | 1157 | 0 | 0 |
| Tolstoi | 1 | m9-25 | 2 | July 27 | 1158 | 0 | 0 |
| Tolstoi | 1 | m10-2 | 2 | July 27 | 1200 | 0 | 0 |
| Tolstoi | 1 | m10-3 | 2 | July 27 | 1201 | 0 | 0 |
| Tolstoi | 1 | m10-4 | 2 | July 27 | 1202 | 0 | 0 |
| Tolstoi | 1 | m10-5 | 2 | July 27 | 1203 | 14 | 0 |
| Tolstoi | 1 | m10-7 | 1 | July 27 | 1205 | 113 | 3 |
| Tolstoi | 1 | m10-8 | 2 | July 27 | 1206 | 26 | 1 |
| Tolstoi | 1 | m10-9 | 2 | July 27 | 1207 | 14 | 0 |
| Tolstoi | 1 | m10-10 | 1 | July 27 | 1208 | 49 | 0 |
| Tolstoi | 1 | m10-11 | 2 | July 27 | 1210 | 31 | 8 |
| Tolstoi | 1 | m10-13 | 1 | July 27 | 1211 | 156 | 5 |
| Tolstoi | 1 | m10-14 | 2 | July 27 | 1212 | 92 | 20 |
| Tolstoi | 1 | m10-15 | 1 | July 27 | 1213 | 118 | 35 |
| Tolstoi | 1 | m10-16 | 1 | July 27 | 1215 | 93 | 7 |
| Tolstoi | 1 | m10-17 | 1 | July 27 | 1216 | 166 | 27 |
| Tolstoi | 1 | m10-19 | 1 | July 27 | 1217 | 34 | 11 |
| Tolstoi | 1 | m10-20 | 1 | July 27 | 1218 | 122 | 36 |
| Tolstoi | 1 | m10-21 | 1 | July 27 | 1220 | 102 | 58 |
| Tolstoi | 1 | m10-22 | 2 | July 27 | 1221 | 32 | 24 |
| Tolstoi | 1 | m10-23 | 2 | July 27 | 1222 | 36 | 39 |

Appendix A. (continued)

| Cliff Section | Tier [a] | Census Photo | Photo Clarity [b] | Date | Time (ADT) | Raw Kittiwake Count (Kr) | Raw Fulmar Count (Fr) |
|---|---|---|---|---|---|---|---|
| Tolstoi | 1 | m10-25 | 2 | July 27 | 1223 | 57 | 69 |
| Tolstoi | 1 | m11-2 | 2 | July 27 | 1225 | 154 | 22 |
| Tolstoi | 1 | m11-3 | 2 | July 27 | 1226 | 53 | 42 |
| Tolstoi | 1 | m11-4 | 2 | July 27 | 1227 | 54 | 15 |
| Tolstoi | 1 | m11-5 | 2 | July 27 | 1228 | 20 | 11 |
| Tolstoi | 1 | m11-7 | 2 | July 27 | 1230 | 14 | 9 |
| Tolstoi | 1 | m11-8 | 3 | July 27 | 1231 | 4 | 22 |
| Tolstoi | 1 | m11-9 | 2 | July 27 | 1232 | 0 | 0 |
| Tolstoi | 1 | m11-10 | 2 | July 27 | 1233 | 46 | 77 |
| Tolstoi | 1 | m11-11 | 2 | July 27 | 1235 | 66 | 91 |
| Tolstoi | 1 | m11-13 | 2 | July 27 | 1236 | 11 | 28 |
| Tolstoi | 1 | m11-14 | 2 | July 27 | 1237 | 0 | 0 |
| Tolstoi | 1 | m11-15 | 2 | July 27 | 1238 | 5 | 0 |
| Tolstoi | 1 | m11-16 | 2 | July 27 | 1240 | 24 | 21 |
| Tolstoi | 1 | m11-17 | 2 | July 27 | 1241 | 185 | 83 |
| Tolstoi | 1 | m11-22 | 3 | July 27 | 1242 | 84 | 55 |
| Tolstoi | 1 | m11-19 | 2 | July 27 | 1243 | 82 | 61 |
| Tolstoi | 1 | m11-20 | 2 | July 27 | 1245 | 111 | 38 |
| Tolstoi | 1 | m11-23 | 2 | July 27 | 1246 | 183 | 55 |
| Tolstoi | 1 | m11-21 | 3 | July 27 | 1247 | 313 | 128 |
| Tolstoi | 1 | m11-25 | 2 | July 27 | 1248 | 539 | 171 |
| Tolstoi | 1 | m12-2 | 3 | July 27 | 1250 | 249 | 166 |
| Tolstoi | 1 | m12-3 | 2 | July 27 | 1251 | 291 | 72 |
| Tolstoi | 1 | m12-4 | 2 | July 27 | 1252 | 210 | 11 |
| Tolstoi | 1 | m12-5 | 2 | July 27 | 1253 | 61 | 0 |
| Tolstoi | 1 | m12-7 | 2 | July 27 | 1255 | 1 | 0 |
| Tolstoi | 1 | m12-8 | 2 | July 27 | 1256 | 0 | 0 |

[a] 1 = 0 - 91.5 m, 2 = >91.5 m - 180 m, 3 = > 180 m.

[b] 1 = sharp, 2 = good, 3 = blurred.

Appendix B. Counts of kittiwakes on land-based plots in 1995. Total counts of adult Red-legged (RLKI) and Black-legged (BLKI) Kittiwakes and nests ("Rnest" and "Bnest" respectively) presented for 54 land-based census plots on St. George Island.

| Area | Plot | Subplot | Tier * | Day | Time | RLKI | Rnest | BLKI | Bnest |
|---|---|---|---|---|---|---|---|---|---|
| High Bluff | 40 | | 3 | July 21 | 1840 | 93 | 12 | 15 | 3 |
| High Bluff | 41 | t | 3 | July 21 | 1800 | 201 | 48 | 14 | 1 |
| High Bluff | 41 | b | 3 | July 21 | 1820 | 163 | 31 | 31 | 9 |
| High Bluff | 42 | a | 3 | July 21 | 1730 | 137 | 40 | 0 | 0 |
| High Bluff | 42 | b | 3 | July 21 | 1730 | 0 | 0 | 0 | 0 |
| High Bluff | 43 | | 3 | July 21 | 1930 | 430 | 183 | 9 | 2 |
| High Bluff | 44 | | 3 | July 21 | 1900 | 423 | 205 | 17 | 6 |
| High Bluff | 54 | a | 3 | July 21 | 1835 | 51 | 5 | 0 | 0 |
| High Bluff | 54 | b | 3 | July 21 | 1828 | 126 | 22 | 0 | 0 |
| High Bluff | 54 | c | 3 | July 21 | 1835 | 128 | 25 | 0 | 0 |
| High Bluff | 55 | | 3 | July 21 | 1850 | 245 | 95 | 7 | 0 |
| High Bluff | 40 | | 3 | July 24 | 1645 | 98 | 17 | 18 | 3 |
| High Bluff | 41 | t | 3 | July 24 | 1636 | 173 | 53 | 22 | 1 |
| High Bluff | 41 | b | 3 | July 24 | 1639 | 166 | 35 | 23 | 11 |
| High Bluff | 42 | a | 3 | July 24 | 1620 | 136 | 38 | 0 | 0 |
| High Bluff | 42 | b | 3 | July 24 | 1623 | 2 | 0 | 0 | 0 |
| High Bluff | 43 | | 3 | July 24 | 1230 | 364 | 159 | 7 | 3 |
| High Bluff | 44 | | 3 | July 24 | 1300 | 358 | 198 | 13 | 6 |
| High Bluff | 54 | a | 3 | July 24 | 1414 | 45 | 3 | 0 | 0 |
| High Bluff | 54 | b | 3 | July 24 | 1419 | 80 | 27 | 0 | 0 |
| High Bluff | 54 | c | 3 | July 24 | 1423 | 132 | 33 | 0 | 0 |
| High Bluff | 55 | | 3 | July 24 | 1430 | 252 | 88 | 3 | 1 |
| High Bluff | 40 | | 3 | July 29 | 1528 | 161 | 17 | 16 | 2 |
| High Bluff | 41 | t | 3 | July 29 | 1544 | 173 | 47 | 31 | 4 |
| High Bluff | 41 | b | 3 | July 29 | 1546 | 165 | 31 | 26 | 11 |
| High Bluff | 42 | a | 3 | July 29 | 1230 | 109 | 59 | 0 | 0 |
| High Bluff | 42 | b | 3 | July 29 | 1230 | 1 | 0 | 0 | 0 |
| High Bluff | 43 | | 3 | July 29 | 1255 | 398 | 199 | 3 | 2 |
| High Bluff | 44 | | 3 | July 29 | 1610 | 418 | 197 | 14 | 7 |
| High Bluff | 54 | a | 3 | July 29 | 1550 | 67 | 6 | 0 | 0 |
| High Bluff | 54 | b | 3 | July 29 | 1555 | 85 | 29 | 0 | 0 |
| High Bluff | 54 | c | 3 | July 29 | 1545 | 117 | 45 | 0 | 0 |
| High Bluff | 55 | | 3 | July 29 | 1515 | 236 | 85 | 7 | 2 |
| High Bluff | 42 | a | 3 | Aug 3 | 1215 | 135 | 57 | 1 | 1 |
| High Bluff | 42 | b | 3 | Aug 3 | 1215 | 1 | 0 | 0 | 0 |
| High Bluff | 43 | | 3 | Aug 3 | 1255 | 455 | 201 | 3 | 2 |
| High Bluff | 44 | | 3 | Aug 3 | 1515 | 461 | 194 | 16 | 6 |
| First Bluff | 1 | a | 2 | July 21 | 2055 | 37 | 5 | 5 | 1 |
| First Bluff | 1 | b | 2 | July 21 | 2100 | 21 | 6 | 0 | 0 |
| First Bluff | 2 | | 2 | July 21 | 2045 | 11 | 2 | 7 | 0 |
| First Bluff | 39 | | 1 | July 21 | 2040 | 15 | 4 | 13 | 1 |
| First Bluff | 1 | a | 2 | July 29 | 1433 | 58 | 4 | 0 | 0 |
| First Bluff | 1 | b | 2 | July 29 | 1435 | 21 | 4 | 2 | 0 |
| First Bluff | 2 | | 2 | July 29 | 1454 | 11 | 2 | 3 | 0 |
| First Bluff | 39 | | 1 | July 29 | 1459 | 53 | 4 | 14 | 3 |
| Zapadni | 8 | | 1 | July 26 | 1746 | 0 | 0 | 0 | 0 |
| Zapadni | 9 | | 1 | July 26 | 1738 | 0 | 0 | 9 | 0 |
| Zapadni | 10 | | 1 | July 26 | 1735 | 2 | 0 | 0 | 0 |
| Zapadni | 11 | | 1 | July 26 | 1730 | 0 | 0 | 0 | 0 |
| Zapadni | 12 | | 1 | July 26 | 1724 | 0 | 0 | 0 | 0 |
| Zapadni | 13o | | 1 | July 26 | 1717 | 0 | 0 | 0 | 0 |

* 1 = 0 - 91.5 m, 2 = >91.5 m - 180 m, 3 = > 180 m.

Appendix B. (continued)

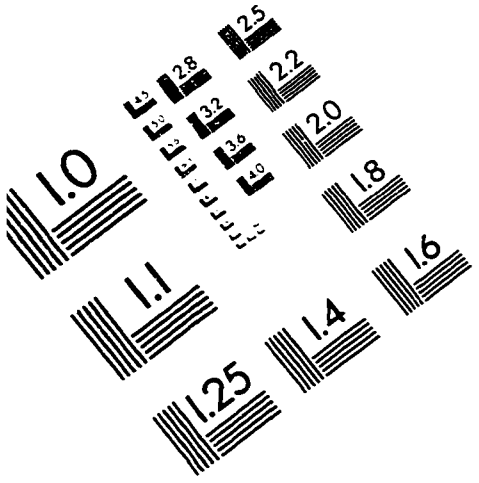
| Area | Plot | Subplot | Tier * | Day | Time | RLKI | Rnest | BLKI | Bnest |
|---|---|---|---|---|---|---|---|---|---|
| Zapadni | 14 | | 1 | July 26 | 1709 | 0 | 0 | 2 | 0 |
| Zapadni | 15 | | 1 | July 26 | 1645 | 16 | 3 | 0 | 0 |
| Zapadni | 16 | | 1 | July 26 | 1635 | 0 | 0 | 4 | 1 |
| Zapadni | 17 | | 1 | July 26 | 1625 | 21 | 4 | 7 | 0 |
| Zapadni | 18 | | 1 | July 26 | 1615 | 2 | 0 | 3 | 0 |
| Zapadni | 19 | | 1 | July 26 | 1605 | 0 | 0 | 6 | 2 |
| Zapadni | 20 | | 1 | July 26 | 1821 | 0 | 0 | 1 | 0 |
| Zapadni | 75 | | 1 | July 26 | 1911 | 0 | 0 | 5 | 1 |
| Zapadni | 8 | | 1 | Aug 1 | 1525 | 3 | 0 | 7 | 0 |
| Zapadni | 9 | | 1 | Aug 1 | 1516 | 0 | 0 | 3 | 0 |
| Zapadni | 10 | | 1 | Aug 1 | 1510 | 0 | 0 | 0 | 0 |
| Zapadni | 11 | | 1 | Aug 1 | 1507 | 0 | 0 | 0 | 0 |
| Zapadni | 12 | | 1 | Aug 1 | 1501 | 1 | 0 | 0 | 0 |
| Zapadni | 13o | | 1 | Aug 1 | 1453 | 0 | 0 | 0 | 0 |
| Zapadni | 14 | | 1 | Aug 1 | 1446 | 0 | 0 | 3 | 0 |
| Zapadni | 15 | | 1 | Aug 1 | 1436 | 19 | 3 | 3 | 0 |
| Zapadni | 16 | | 1 | Aug 1 | 1432 | 0 | 0 | 4 | 1 |
| Zapadni | 17 | | 1 | Aug 1 | 1428 | 11 | 4 | 6 | 0 |
| Zapadni | 18 | | 1 | Aug 1 | 1401 | 1 | 0 | 5 | 0 |
| Zapadni | 19 | | 1 | Aug 1 | 1353 | 1 | 0 | 11 | 3 |
| Zapadni | 20 | | 1 | Aug 1 | 1349 | 2 | 0 | 0 | 0 |
| Zapadni | 75 | | 1 | Aug 1 | 1630 | 2 | 0 | 9 | 1 |
| Red Bluff | 21 | | 1 | July 19 | 1530 | 0 | 0 | 3 | 1 |
| Red Bluff | 22 | | 1 | July 19 | 1535 | 0 | 0 | 0 | 0 |
| Red Bluff | 23 | | 1 | July 19 | 1540 | 12 | 2 | 0 | 0 |
| Red Bluff | 24 | t | 1 | July 19 | 1555 | 1 | 0 | 19 | 4 |
| Red Bluff | 24 | m | 1 | July 19 | 1600 | 0 | 0 | 0 | 0 |
| Red Bluff | 25 | | 1 | July 19 | 1610 | 8 | 3 | 7 | 1 |
| Red Bluff | 26 | | 1 | July 19 | 1615 | 0 | 0 | 2 | 0 |
| Red Bluff | 27 | t | 1 | July 19 | 1620 | 23 | 3 | 21 | 1 |
| Red Bluff | 27 | b | 1 | July 19 | 1625 | 14 | 3 | 6 | 0 |
| Red Bluff | 28 | l | 1 | July 19 | 1630 | 7 | 2 | 10 | 0 |
| Red Bluff | 28 | m | 1 | July 19 | 1635 | 0 | 0 | 0 | 0 |
| Red Bluff | 29 | | 1 | July 19 | 1645 | 15 | 4 | 0 | 0 |
| Red Bluff | 30 | l | 1 | July 19 | 1650 | 0 | 0 | 0 | 0 |
| Red Bluff | 30 | r | 1 | July 19 | 1655 | 9 | 0 | 10 | 3 |
| Red Bluff | 31 | | 1 | July 19 | 1705 | 0 | 0 | 1 | 0 |
| Red Bluff | 32 | t | 1 | July 19 | 1710 | 0 | 0 | 0 | 0 |
| Red Bluff | 32 | b | 1 | July 19 | 1710 | 0 | 0 | 0 | 0 |
| Red Bluff | 33 | a | 1 | July 19 | 1725 | 28 | 4 | 3 | 0 |
| Red Bluff | 33 | b | 1 | July 19 | 1723 | 7 | 0 | 0 | 0 |
| Red Bluff | 33 | c | 1 | July 19 | 1721 | 18 | 3 | 5 | 0 |
| Red Bluff | 33 | d | 1 | July 19 | 1719 | 10 | 2 | 4 | 0 |
| Red Bluff | 34 | | 1 | July 19 | 1815 | 9 | 3 | 0 | 0 |
| Red Bluff | 35 | t | 1 | July 19 | 1835 | 12 | 0 | 22 | 1 |
| Red Bluff | 35 | b | 1 | July 19 | 1840 | 22 | 5 | 5 | 1 |
| Red Bluff | 36 | | 1 | July 19 | 1900 | 2 | 0 | 1 | 0 |
| Red Bluff | 37 | t | 1 | July 19 | 1930 | 10 | 2 | 12 | 3 |
| Red Bluff | 37 | b | 1 | July 19 | 1935 | 3 | 0 | 3 | 1 |
| Red Bluff | 38 | t | 1 | July 19 | 1950 | 1 | 0 | 0 | 0 |
| Red Bluff | 38 | m | 1 | July 19 | 1955 | 2 | 0 | 4 | 1 |
| Red Bluff | 38 | b | 1 | July 19 | 1945 | 1 | 0 | 9 | 0 |
| Red Bluff | 21 | | 1 | Aug 5 | 1820 | 0 | 0 | 5 | 0 |
| Red Bluff | 22 | | 1 | Aug 5 | 1825 | 0 | 0 | 0 | 0 |
| Red Bluff | 23 | | 1 | Aug 5 | 1830 | 19 | 2 | 3 | 0 |
| Red Bluff | 24 | t | 1 | Aug 5 | 1850 | 3 | 0 | 34 | 3 |
| Red Bluff | 24 | m | 1 | Aug 5 | 1855 | 0 | 0 | 0 | 0 |

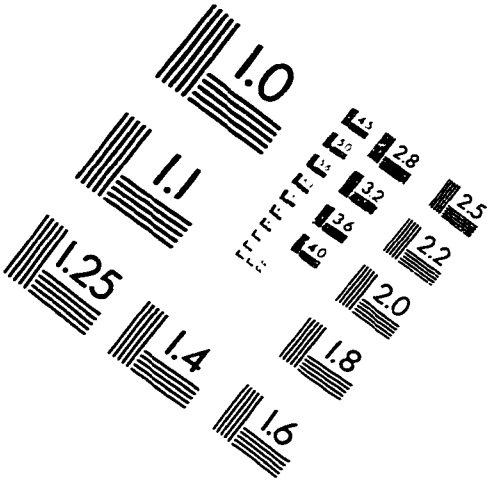
Appendix B. (continued)

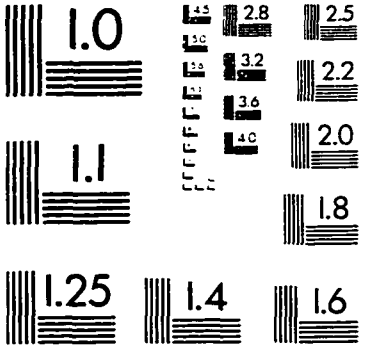
| Area | Plot | Subplot | Tier * | Day | Time | RLKI | Rnest | BLKI | Bnest |
|---|---|---|---|---|---|---|---|---|---|
| Red Bluff | 25 | | 1 | Aug 5 | 1925 | 7 | 2 | 16 | 4 |
| Red Bluff | 26 | | 1 | Aug 5 | 1920 | 0 | 0 | 5 | 0 |
| Red Bluff | 27 | t | 1 | Aug 5 | 1930 | 30 | 3 | 22 | 3 |
| Red Bluff | 27 | b | 1 | Aug 5 | 1935 | 21 | 2 | 4 | 0 |
| Red Bluff | 28 | l | 1 | Aug 5 | 1940 | 4 | 1 | 9 | 2 |
| Red Bluff | 28 | m | 1 | Aug 5 | 1945 | 1 | 0 | 7 | 1 |
| Red Bluff | 29 | | 1 | Aug 5 | 1950 | 27 | 6 | 3 | 1 |
| Red Bluff | 30 | l | 1 | Aug 5 | 2000 | 0 | 0 | 1 | 0 |
| Red Bluff | 30 | r | 1 | Aug 5 | 2005 | 6 | 1 | 18 | 1 |
| Red Bluff | 31 | | 1 | Aug 5 | 2010 | 0 | 0 | 5 | 0 |
| Red Bluff | 32 | t | 1 | Aug 5 | 2015 | 0 | 0 | 0 | 0 |
| Red Bluff | 32 | b | 1 | Aug 5 | 2015 | 0 | 0 | 0 | 0 |
| Red Bluff | 33 | a | 1 | Aug 5 | 2025 | 76 | 14 | 15 | 3 |
| Red Bluff | 33 | b | 1 | Aug 5 | 2030 | 1 | 0 | 7 | 2 |
| Red Bluff | 33 | c | 1 | Aug 5 | 2035 | 3 | 1 | 1 | 0 |
| Red Bluff | 33 | d | 1 | Aug 5 | 2035 | 8 | 4 | 3 | 0 |
| Red Bluff | 34 | | 1 | Aug 5 | 2120 | 5 | 2 | 0 | 0 |
| Village | 58 | a | 1 | July 20 | 1605 | 107 | 18 | 111 | 14 |
| Village | 58 | b | 1 | July 20 | 1630 | 42 | 2 | 163 | 23 |
| Village | 58 | c | 1 | July 20 | 1650 | 102 | 9 | 281 | 79 |
| Village | 59 | a | 1 | July 20 | 1930 | 65 | 8 | 138 | 8 |
| Village | 59 | b | 1 | July 20 | 1915 | 0 | 0 | 0 | 0 |
| Village | 59 | c | 1 | July 20 | 1830 | 0 | 0 | 105 | 5 |
| Village | 81 | a | 1 | July 22 | 1345 | 13 | 1 | 38 | 6 |
| Village | 81 | b | 1 | July 22 | 1320 | 102 | 17 | 40 | 6 |
| Village | 81 | c | 1 | July 22 | 1230 | 35 | 3 | 40 | 13 |
| Village | 81 | d | 1 | July 22 | 1245 | 71 | 8 | 58 | 11 |
| Village | 81 | a | 1 | July 25 | 1610 | 15 | 2 | 64 | 14 |
| Village | 81 | b | 1 | July 25 | 1650 | 164 | 27 | 89 | 4 |
| Village | 81 | c | 1 | July 25 | 1630 | 35 | 3 | 29 | 12 |
| Village | 81 | d | 1 | July 25 | 1615 | 97 | 11 | 78 | 3 |
| Village | 81 | a | 1 | July 28 | 1515 | 16 | 1 | 46 | 12 |
| Village | 81 | b | 1 | July 28 | 1500 | 116 | 39 | 48 | 10 |
| Village | 81 | c | 1 | July 28 | 1445 | 37 | 6 | 37 | 11 |
| Village | 81 | d | 1 | July 28 | 1430 | 50 | 7 | 54 | 10 |
| Tolstoi | 45 | | 1 | July 26 | 1935 | 0 | 0 | 4 | 0 |
| Tolstoi | 46 | | 1 | July 26 | 1920 | 1 | 0 | 27 | 1 |
| Tolstoi | 47 | | 1 | July 26 | 1915 | 5 | 3 | 16 | 0 |
| Tolstoi | 48 | | 1 | July 26 | 1910 | 4 | 0 | 6 | 0 |
| Tolstoi | 49 | | 1 | July 26 | 1900 | 0 | 0 | 0 | 0 |
| Tolstoi | 50 | | 1 | July 26 | 1900 | 0 | 0 | 0 | 0 |
| Tolstoi | 51 | | 1 | July 26 | 1850 | 1 | 0 | 2 | 0 |
| Tolstoi | 52 | | 1 | July 26 | 1840 | 69 | 16 | 56 | 7 |
| Tolstoi | 53 | | 1 | July 26 | 1955 | 71 | 32 | 225 | 83 |
| Tolstoi | 45 | | 1 | Aug 1 | 1550 | 0 | 0 | 4 | 0 |
| Tolstoi | 46 | | 1 | Aug 1 | 1530 | 2 | 1 | 34 | 3 |
| Tolstoi | 47 | | 1 | Aug 1 | 1520 | 0 | 0 | 10 | 0 |
| Tolstoi | 48 | | 1 | Aug 1 | 1510 | 5 | 0 | 12 | 0 |
| Tolstoi | 49 | | 1 | Aug 1 | 1505 | 0 | 0 | 0 | 0 |
| Tolstoi | 50 | | 1 | Aug 1 | 1500 | 0 | 0 | 0 | 0 |
| Tolstoi | 51 | | 1 | Aug 1 | 1455 | 1 | 0 | 1 | 0 |
| Tolstoi | 52 | | 1 | Aug 1 | 1435 | 62 | 14 | 63 | 5 |
| Tolstoi | 53 | | 1 | Aug 1 | 1610 | 67 | 29 | 251 | 87 |

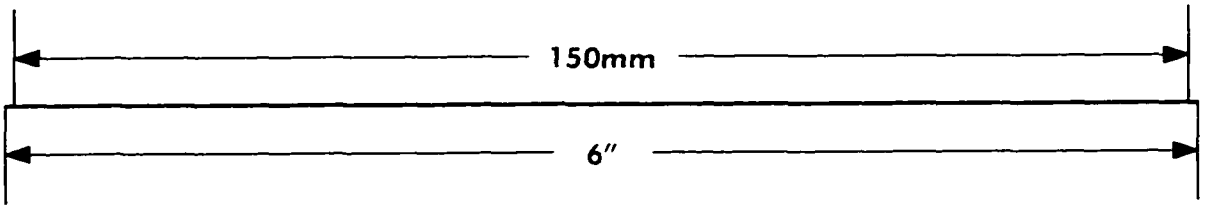
* 1 = 0 - 91.5 m, 2 = >91.5 m - 180 m, 3 = > 180 m.

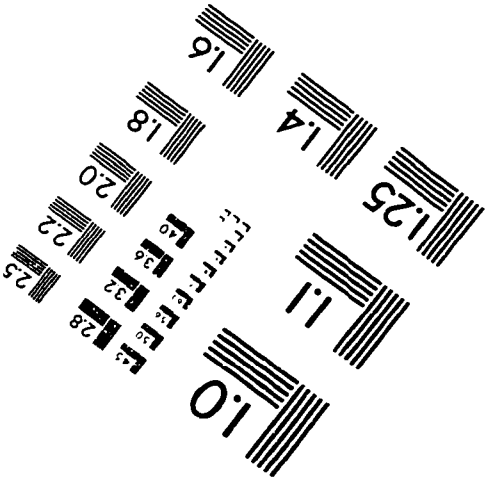
# IMAGE EVALUATION TEST TARGET (QA-3)

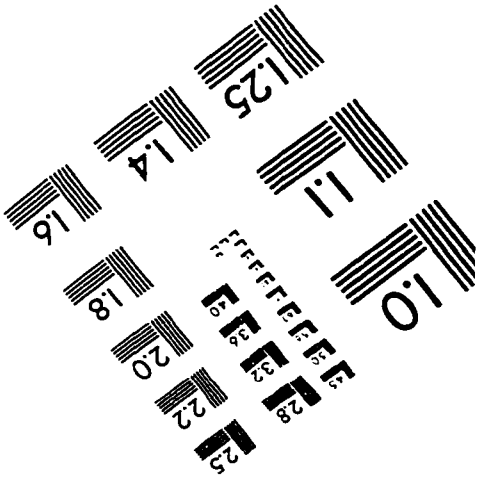
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Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989